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RESEARCH INSTITUTE, NEW DELHI

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ECOLOGY

ALL FORMS OF LIFE IN RELATION TO ENVIRONMENT

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CONTINUING THE PLANT WORLD

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ECOLOGY

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No. 1

ANIMAL RELATIONSHIPS OF GREAT SALT LAKE¹

ANGUS M. WOODBURY

University of Utah

The Great Salt Lake, with its saline content approaching saturation, presents a hostile environment to most living organisms, both within the water and upon the nearby shores. Those who would survive the rigors of this aquatic desert must either be equipped to meet the exactions imposed or to avoid them.

The problem of meeting the peculiarities of the environment is largely physiological—that of extracting moisture from a salt solution. This problem varies not only from time to time with the rise and fall of the lake level and its consequent dilution and concentration but also from place to place where dilution occurs by the inpouring of fresh-water streams and underground seepage. The paucity of life forms actually living within the lake water is undoubtedly due to these severe restrictions.

The principal food-makers of the lake are blue-green algae including several colonial forms of the genus *Aphanotheca* which produce salmon colored gelatin-like masses, especially near shore, diatoms of the genera *Navicula* and *Cymbella*, two flagellates of the genus *Chlamydomonas*, and several others of lesser importance. These are undoubtedly the food base for a very limited fauna of protozoans and invertebrates which can withstand immersion in the water of the lake. A rhizopod of the genus *Amoeba* and a ciliate of the genus *Uroleptus* are reported to occur, undoubtedly in vast numbers although invisible to the eye.

Of the visible forms, the brine shrimp, *Artemia gracilis* Verrill, and two brine flies, *Ephydra gracilis* Packard and *Ephydra hians* Say are common inhabitants of the lake. So far as known, no parasites have been able to follow them into the brine. Freed from parasites, these arthropods have been enabled to multiply with little or no molestation to the limit of the food supply,

¹ Paper read at a symposium of the problems of the Great Salt Lake at the meetings of the Pacific Division of the American Association for the Advancement of Science, June, 1933.

Accession No 3722726

presumably provided principally by the blue-green algae. They occur in enormous numbers in many parts of the lake, especially near the shore where the algae are abundant. It is not quite clear how the three species can maintain themselves in apparent competition with one another. There is a need for further study to elucidate the niche filled by each one.

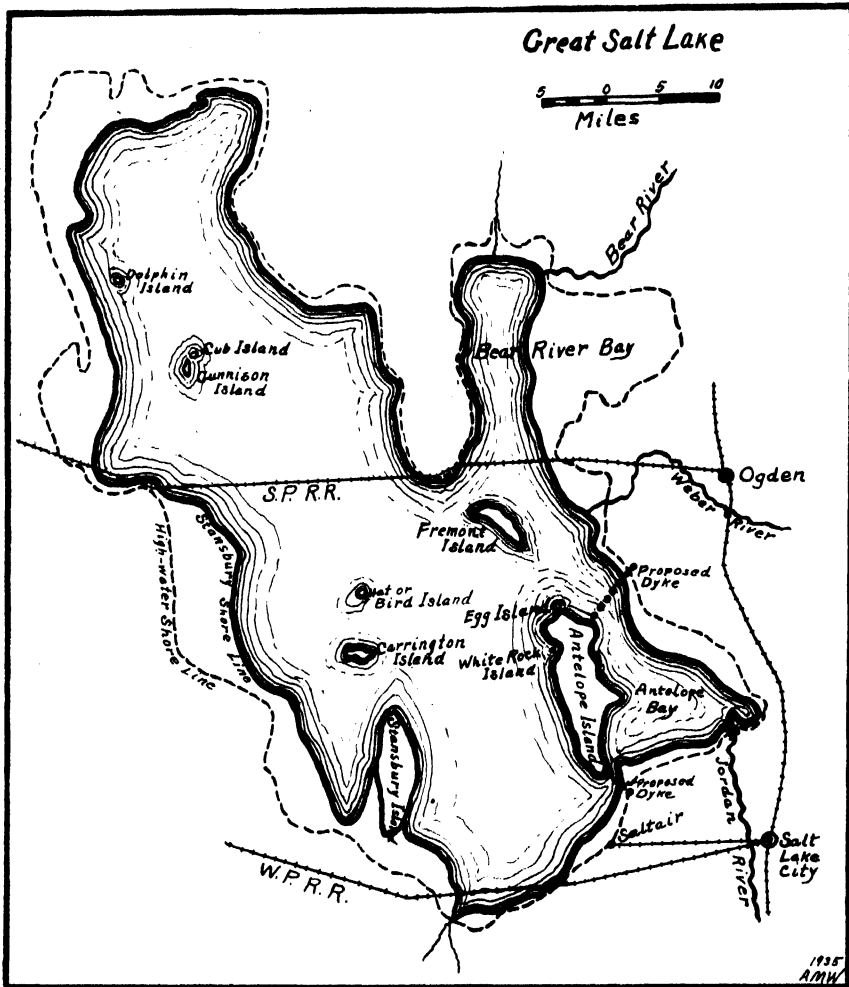


FIG. 1. Great Salt Lake, Utah.

The crustacean, *Artemia*, spends its entire life cycle in the water, growing to sexual maturity in about three weeks. It propagates parthenogenetically as well as by means of fertilized eggs. It appears to offer a fertile field of inquiry into the genetic relationships. According to Jensen ('18), the shrimp passes the winter in the egg stage. The egg hatches in the early spring and the embryo develops into a free-swimming nauplius which passes through a series of stages before reaching maturity.

Jensen's experiments showed that the eggs developed better in water

diluted to a specific gravity of 1.027 to 1.044 than in normal lake water with gravity about 1.13. The inference is that the eggs would develop better in the dilutions due to the spring high-water inflow, especially around the mouths of the streams, than in the more dense solutions farther out or at low water stages. The summer months reveal enormous numbers of adults which disappear again as winter approaches, probably being killed by the lowering temperature.

The insects as would be expected, leave the water in the adult stage. The eggs, larvae and pupae, however, are strictly aquatic. Both species of these brine flies are peculiarly adapted in the larval stages to a water existence by having the breathing tube transformed into a tracheal gill so they do not need to come to the surface to breathe.

When mature, the larvae attach themselves to the bottom with the prolegs and pupate. As the pupa shrinks, the vacant space within the pupal case is filled with gas, making it buoyant. Disturbances in the water loosen large numbers of the pupae and they float to the top. The drift collects them together in favorable places, sometimes producing great windrows along the edge of the water and on the nearby shore. These were formerly gathered by the Indians as a source of food.

In emerging from the pupal case, the adults are borne to the surface of the water by the gas bubble within the case. They collect in huge numbers on the surface of the water, especially near shore and often extend some distance up onto the land. Aldrich estimated a population of 25 per square inch or 370 million flies per mile of beach.

Both the pupae and adults undoubtedly furnish an important food supply, especially to spiders of the water edge and to many kinds of birds. Brewer (as reported by Aldrich ('12), p. 90) quotes an old time hunter (1863) to the effect that everything fattens in the season of koo-tsabe (referring to the pupae); the ducks get very fat but their flesh tastes unpleasantly from it, and the Indians get fat and sleek.

Fremont ('45), on September 9, 1843, reported a bank on the beach of Fremont Island 10-20 feet wide covered to a depth of 7 to 12 inches "entirely of the larvae of insects, or, in common language, of the skins of worms, about the size of a grain of oats, which had been washed up by the waters of the lake." He no doubt referred to pupae of the brine flies, and the description is still valid to-day.

Captain Stansbury ('52) on April 11, 1850, seven years later, also refers to these brine flies. He states: "In wading to the shore, we struggled through a deep soft dark coloured mass . . . which upon examination proved to consist almost solely of the larvae of insects lying upon the bottom, producing when disturbed, a most offensive and nauseous odour. The mass was more than a foot in thickness and extended several yards from the shore."

VERTEBRATES

No vertebrates have been able to succeed within the briny waters of the lake, although certain of the birds, notably gulls, grebes, phalaropes and ducks utilize the surface, and many of them feed upon the invertebrates of the lake. The brine, however, has greatly affected the distribution of the vertebrates especially those that inhabit the islands and those that approach the shores.

The physiologically dry salty flats near the shores definitely control and limit the types of plants that can succeed upon them, and the vegetation in turn helps to limit the type of animals that can persist under its influence. A crop of insects adapted to take their living from the succulent plants furnishes a food base for spiders, horned lizards and certain insectivorous birds. The seeds and foliage of the plants are utilized directly by a ground squirrel of the genus *Citellus*, and by certain birds, especially the desert horned lark and the Nevada Savannah Sparrow.

The increasing concentration of the water of streams as they approach the lake undoubtedly affects the fauna by becoming more and more restrictive until, mixing with the lake water, it finally becomes exclusive. The detail of this transformation seems not to be fully understood and needs further study but it is known that carp descending the streams too far perish before reaching the concentrated lake water.

Artificial lakes made by dyking produce interesting problems only incompletely studied. The storing of water on the salty flats, and its discharge into the lake carrying the dissolved salts with it is a method of reclamation tending toward the production of fresh water lakes with a greatly increased capacity for the sustenance of life. The Bear River Refuge at the northeast corner of the lake at the mouth of Bear River, is an experiment on a large scale to provide for a wholesale increase in the aquatic birds of the region. This Federal enterprise, covering some 65,000 acres of land and containing some 19 miles of main dykes and several miles of subdivisional dykes separating the lake into five units, offers an opportunity to study the transitional stages and the advantages of such reclamation.

There is little doubt that the Bear River delta has long been a mecca for aquatic birds. Fremont ('45) visited the delta on September 3, 1843 and describes the scene thus: "The water fowl made this morning a noise like thunder. A pelican (*Pelecanus onocrotalus*) was killed as he passed by, and many geese and ducks flew over the camp. Descending the river for about three miles in the afternoon, we found a bar to any further travelling in that direction—the stream being spread out in several branches, and covering the low grounds with water, where the miry nature of the bottom did not permit any further advance. We were evidently on the border of the lake, although the rushes and canes which covered the marshes prevented any view; and we accordingly encamped at the little delta which forms the mouth

of Bear River; a long arm of the lake stretching up to the north between us and the opposite mountains. The river was bordered with a fringe of willows and canes, among which were interspersed a few plants; and scattered about on the marsh was a species of *Uniola*, closely allied to *U. spicata* of our sea coast. The whole morass was animated with multitudes of water fowl, which appeared to be very wild—rising for the space of a mile round about at the sound of a gun, with a noise like distant thunder. Several of the people waded out into the marshes, and we had to-night a delicious supper of ducks, geese, and plover."

Captain Stansbury ('52), on October 22, 1849, looking over Bear River Bay from the east side of Promontory point remarked that it "was covered by immense flocks of wild geese and ducks among which many swans were seen, being distinguishable by their size and the whiteness of their plumage. I had seen large flocks of these birds before, in various parts of our country, and especially upon the Potomac, but never did I behold any thing like the immense numbers here congregated together. Thousands of acres, as far as the eye could reach, seemed literally covered with them, presenting a scene of busy, animated cheerfulness, in most graceful contrast with the dreary, silent solitude by which we were immediately surrounded."

Undoubtedly the deltas formed by other rivers notably the Weber and Jordan, were similarly attractive to the aquatic birds. At the mouth of the Weber River on September 8, 1843, Fremont remarked: "geese and ducks enough had been killed for an abundant supper at night and for breakfast next morning. The stillness of the night was enlivened by millions of water fowl." The next day, down on the low water shore of the lake, he remarked: "All this place was absolutely covered with flocks of screaming plover."

Stansbury, on April 4, 1850, 7 years later states that "Innumerable flocks of ducks, geese, white swans, and long-legged plover were seen during the day, congregated around the shallows at the mouth of the Jordan.

These meager pictures of Fremont and Stansbury raise the question of whether or not and how much the diversion of water, the grazing of livestock, and the hunting of game birds has affected the supply of birds on the edges of the lake. The probability is that they have been much reduced in numbers.

The duck sickness may have helped in this reduction. The loss of a half million ducks in one season is a serious problem. Three theories have been advanced to account for the disease: (1) an alkaline poisoning due to an excess of alkali in the diet, (2) lead poisoning due to picking up the shot from hunters shells, and (3) a bacterial poisoning from botulinus germs incubated in the mud. Later investigations seem to confirm the theory that botulinus poisoning is the chief cause. It is known, however, that the ducks usually recover if transferred from the alkaline pools and flats to clean fresh water. It still remains to be seen whether or not the Bear River Refuge, through transforming the area into fresh water lakes, will minimize the sickness.

Many gun clubs at the mouths of the Jordan and Weber rivers have

undertaken the reclamation of similar areas on a smaller scale. These have principally to do with the deltas and the lowland marshes and not with the lake itself. There is now a proposal under consideration for dyking that part of the lake lying east of Antelope Island and transforming it into a fresh water lake. Undoubtedly such a body of water would be diluted by the fresh water from the streams that flow into it, but the time required to dilute it sufficiently to permit the establishment of food plants and the consequent train of animal life is problematical. There are further questions of the effect of the German carp upon the establishment of such food plants, the role of their competition with wild fowl for such food and the development of the botulinus poisoning on mud flats left by the fluctuating water level. If these problems can be properly solved, such a lake would add much to the security of the wild fowl and other aquatic birds.

The large islands of the lake, Stansbury and Antelope, have a fauna essentially similar to that of the surrounding region. Captain Stansbury ('52) reports on June 15, 1850, seeing antelope on the island of that name. This island would make an ideal sanctuary for this vanishing mammal if it could be brought under public control. If done, it could readily be administered in correlation with the proposed fresh-water lake east of the island.

Four of the smaller islands of the lake are unique in having a special fauna of birds during the nesting season. These include in order of size and importance, Gunnison, Hat, Egg and White Rock islands. The California gulls inhabit all of these islands; the white pelicans the two larger islands, Gunnison and Hat; the Treganza blue heron the three larger islands, Gunnison, Hat and Egg; while the double-crested cormorants are limited to Egg Island only. Behle ('32) estimated a total of 80,000 gulls, 10,600 pelicans, 96 herons and 100 cormorants nesting on the islands of Great Salt Lake in 1932.

The first picture of the rookeries of the islands of Great Salt Lake given us by Captain Stansbury in 1851 is slightly different. Apparently no birds nested on Hat Island at that time, since he described the island carefully but does not mention any birds. He did not visit White Rock Island. He does, however, describe the birds on Gunnison and Egg Islands. Gulls and pelicans were numerous on both islands, whereas the cormorants and herons appear to have been limited to Egg Island. The pelicans no longer nest on Egg Island but have adopted Hat Island as have the gulls and herons also. Caspian Terns at one time also nested there.

With reference to fluctuations in numbers, Behle ('32) shows that the herons have decreased in numbers from 400 in 1915 on Hat Island to 96 on all the islands in 1932, and the cormorants on Egg Island have decreased from 500 in 1915 to 100 in 1932. Definite figures for the gulls and pelicans are lacking but apparently they are holding their own. The continuous hostility of certain groups of sportsmen against fish-eating birds, the illegal killings and the recent raids of heron and cormorant rookeries in the sur-

rounding region are undoubtedly some of the more important factors in driving the numbers of these birds downward toward the vanishing point.

Behle's studies in 1932 showed that the herons, cormorants and pelicans feed their young almost exclusively upon fish, the type being determined by the locality from which the fish are obtained. Since there are no fish at all in Great Salt Lake, the adult birds must bring the fish from the streams and lakes within flying distance of the islands. The chief sources of supply are the lower reaches of the Jordan, Weber and Bear rivers, including Utah Lake and the units of the Bear River Refuge. These birds are strong fliers and the daily foraging expeditions usually range from 30 to 100 miles each way.

The fish inhabiting these feeding waters are mostly non-game slow-moving fish such as carp, chubs and suckers, and these form the bulk of the food gathered by these birds. In a few places, such as at Utah Lake, these fish come in competition with such game fish as trout, catfish and bass, which being more active, are less often caught by the birds. There appear to be two definite advantages from this situation. First, the reduction of the non-game fish favors the development of game fish where they are in competition. Second, the reduction in numbers of the vegetarian carp favors the development of the food plants in the waters they inhabit.

These islands present almost ideal conditions for bird rookeries despite the distance to food. They afford protection from carnivorous mammals, privacy from disturbance from everything except occasional visits of man, and ideal nesting sites for aquatic birds since the islands are low and afford ready access for the young to the water. Here then is an ideal situation for a bird rookery sanctuary.

This seems to be especially necessary in view of the destruction of the white pelican elsewhere. Since the national government gives this bird no federal protection, it faces a real danger. This should certainly be avoided despite its questionable economic status elsewhere, as in Yellowstone Lake where it feeds almost exclusively upon trout. Here, however, is a chance to maintain the species in a region, where, if not positively beneficial, its benefits at least offset its disadvantages.

Such a sanctuary should, in my opinion, be controlled by the Federal Government on the theory that these islands are migratory bird breeding grounds in strategic positions and essential to the proper propagation of the species involved.

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A CLIMAX FOREST COMMUNITY ON EAST TIONESTA CREEK IN NORTHWESTERN PENNSYLVANIA

A. F. HOUGH

*Allegheny Forest Experiment Station*¹

The original forest growth of Pennsylvania has almost vanished due to clearing for agriculture, commercial logging, and forest fires, since the advent of the white settler. We are now faced with the problem of rehabilitating and managing our second-growth forest stands for future cellulose production, watershed protection, wild life, and recreation. Both foresters and plant ecologists realize the dynamic nature of these young, developing stands of second and third growth forest. There can be no doubt that Nature, barring serious further interference by man, is working toward the reestablishment of a climatic climax stage. Methods of speeding or modifying the slow natural selection of species practiced by Nature, will be most successful when the forester understands the tendencies of plant succession and applies them in producing a forest best suited to the climate and soil of a given area.

The climax virgin forest (fig. 1), in which are recorded and integrated all the multitude of environmental factors operative through its long centuries of development, is the final result of a gigantic experiment of plant evolution and adaptation. It is to such an area that we go for knowledge of the tree species and kind of forest organism capable of using the site to best advantage. A study of the ecological structure of such a forest should give information of great value in the future management of large acreages of second-growth stands. Recognition of the great research value of the East Tionesta virgin forest resulted in the present study by the Allegheny Forest Experiment Station, which was conducted in 1930 on 1200 acres.

THE EAST TIONESTA AREA

Location and Ownership

The largest single tract of virgin forest in the Eastern United States, between the Adirondacks and the Great Smoky Mountains, is located on the east and south branches of Tionesta Creek in Warren and McKean counties within the Allegheny National Forest (fig. 2). This tract was over 6,800 acres in area before the logging season of 1930 but has since been reduced to a 3,836-acre tract held in Federal ownership, to be designated as a Natural

¹ Maintained by the United States Forest Service at Philadelphia, Pennsylvania, in cooperation with the University of Pennsylvania.

Area for science, research, and education. This purchase was made from the Central Pennsylvania Lumber Company of Sheffield, Pennsylvania, in November, 1934.

Physiography and Geology

Warren and McKean counties lie to the northwest of the Allegheny Front which in Pennsylvania divides the Appalachian Plateau from the folded region of ridges and valleys called the Appalachian Valley. The plateau of these



FIG. 1. A climax forest of eastern hemlock, *Tsuga canadensis* (L.) Carr., of stately form, screened from below by the foliage of beech, *Fagus grandifolia* Ehr.

two counties has an elevation of 1,800 to 2,400 feet above sea level and has been extensively and deeply dissected by stream action into steep-sided, narrow valleys with remnants of the former peneplain between them. (Bowman, '11.) This tract has narrow V-shaped valleys with a depth of 400–500 feet and is drained by Tionesta Creek which flows southwest into the Allegheny River. A geological description of the Warren quadrangle has been made by Butts ('10).

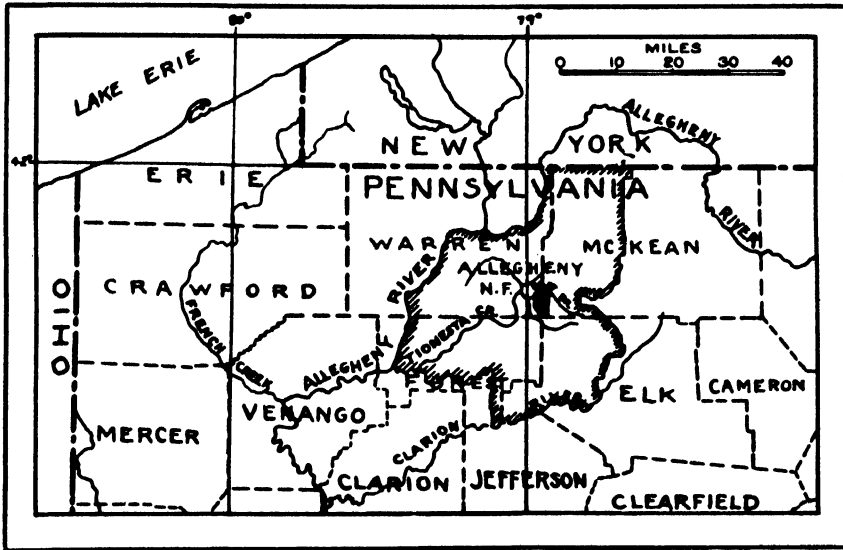


FIG. 2. The East Tionesta Tract, shown in solid black, with reference to drainage and political subdivisions.

Soils

Soil types mapped are the Leetonia stony loam, Cooksport silt loam, Tionesta stony silt loam,² Tionesta silt loam, DeKalb silt loam, DeKalb stony silt loam (steep phase), and Atkins silt loam. A description of the soil types will appear in a later publication.

Fire

An examination of the upper soil layers at 2-chain intervals showed no traces of charcoal and indicates that the 1,200 acres carefully studied has had few if any fires. No definite fire scars were found on 30 hemlock stumps which were 149 to 445 years old, in the Pigeon Run drainage. This absence of fire is a noteworthy feature and is probably due to the moist nature of the forest floor, lack of inflammable undergrowth, and isolation of the area from the dryer south-facing slopes by the stream bed of the creek. That fire, far

² The Tionesta soil series is a series which originated with this survey. So far as is known no such soil has ever been correlated by the Bureau of Chemistry and Soils of the U. S. Department of Agriculture.

from being completely absent from Tionesta, has been of great ecological importance, is shown by the present condition of a swath, south of the area examined, which was first visited by wind and then fire-swept, about 60 years ago. The ridge south of Cherry Run formerly supported a dense stand of hemlock and hardwoods; many rotting and fire-charred hemlock boles with upturned roots are mute evidence of its former glory. Fire destroyed all hemlock seedlings and seed trees; the stand is now composed of hardwoods such as red maple, black cherry, yellow and black birch. The return of this stand to a climax condition has been greatly delayed by the heavy burn following windthrow.

Recent Climate

Climatological charts prepared by Morey ('31) indicate that the average climatic conditions for East Tionesta are similar to those at Hearts Content (Lutz, '30). The average annual precipitation is 42 inches of which 16 inches falls between June and September inclusive. The average annual temperature is 46–47° F. and average summer temperature 66° F. The average length of growing season is 135–138 days. The average date of the last killing frost in the spring is on May 28 and of the first killing frost in autumn on September 25. In order to obtain data on the past yearly climatic conditions as shown by tree growth rings, sections have been cut from 5 hemlock ranging from 200 to 560 years of age. These are being studied by Dr. A. E. Douglass of the University of Arizona, Tucson, Arizona.

Past Climate and Tree Distribution

Jennings ('27) and Berry ('23) believe that the major part of our present day forest flora had developed during the Tertiary period and that such changes as have occurred since that time have chiefly influenced its distribution.

"The effect of the periods of glaciation on this flora was to create in front of the ice, much the same belts or zones of vegetation that now cross the northern part of North America in a general east-west direction; a narrow belt of arctic tundra near the ice edge, boreal conifers next, with a mixed transition forest of white pine, hemlock, sugar maple, beech, etc., to the south, and a wide zone of deciduous hardwoods still further south. As the ice of the last glacial stage retreated, perhaps 40,000 years ago, these zones of vegetation expanded and followed each other northward except where local conditions of topography, exposure, cold soils, cold spring waters, or high altitude, have kept the southern plants from taking possession" (Jennings, '27).

That there is a tendency for the oaks, white pine, and chestnut, to occur on the south-facing slopes in this East Branch of Tionesta area has been observed. The north slopes and plateau top are almost exclusively covered with a hemlock-beech forest containing remnants of a more northern flora such as *Lycopodium lucidulum*, *Taxus canadensis*, and *Viburnum alnifolium*.

THE VEGETATION OF EAST TIONESTA

In 1930 the Allegheny Forest Experiment Station examined the vegetation on 651 square chain (tenth acre) plots along cruise lines in the East Tionesta virgin forest. This sample represented a 5-percent cruise of 1,200 acres, practically all of which has since been logged. Each square chain of the strip was tallied separately to facilitate statistical computations. The tally included the diameter at breast height (4.5 feet above the ground and hereafter abbreviated d.b.h.), of all trees 3.6 inches d.b.h. or larger, and the estimated height class of each tree, (5 divisions defined in table I), based on total height. Measurements were taken with the diameter tape and all distances along the strip were chained with a steel tape. Height class estimates were checked occasionally with the Abney level.

Small trees between 0.6-inch and 3.5 inches in d.b.h. were tallied on a transect 10 links (6.6 feet) wide along the center of each chain length. Reproduction under 0.6 inch d.b.h. was likewise tallied by 1 foot height classes on this transect. The shrubby and herbaceous vegetation was recorded by number of individuals on a quadrat 6.6×6.6 feet in size (0.001 acre) at the end of every second chain. General descriptive notes covering the condition and history of the forest and soils were also taken at this point.

Five hundred and eighty-seven of the 0.1-acre tallies have been used as a sample of unburned and uncut virgin forest. This sample was subdivided on the basis of topography into 39.7 acres on the ridge tops and plateau, 15.9 acres on the middle slopes, and 3.1 acres of lower slope.

All tree species are listed according to the nomenclature of Sudworth ('27); shrubs and herbs that of Gray's Manual (Robinson and Fernald, '08).

Dominant Stand

Seen from a distance the dark hemlock crowns dominate the physiognomy of this forest. To an observer within the stand beech seems most prominent because of the greater number of stems per acre and screening of the dominant hemlock crowns by the foliage of this and other understory species (fig. 1).

The relative importance of the dominant arborescent species, (trees 10 inches d.b.h. and over), is graphically shown in figure 3, using the method described by Lutz ('30). The same 4 criteria of abundance, frequency, number of size classes represented, and basal area in square feet per acre, are used in order that direct comparison with the Hearts Content "phytographs" may be made.

Examination of these "phytographs" reveals that hemlock and beech are outstanding species in the dominant tree cover on plateau, middle and lower slopes. Sugar maple ranks third on the plateau but falls below yellow birch on middle and lower slopes. The ability of most species found in the dominant cover to perpetuate themselves is shown by occurrence in all size classes from small reproduction to large trees. Red oak, cucumber magnolia, chest-

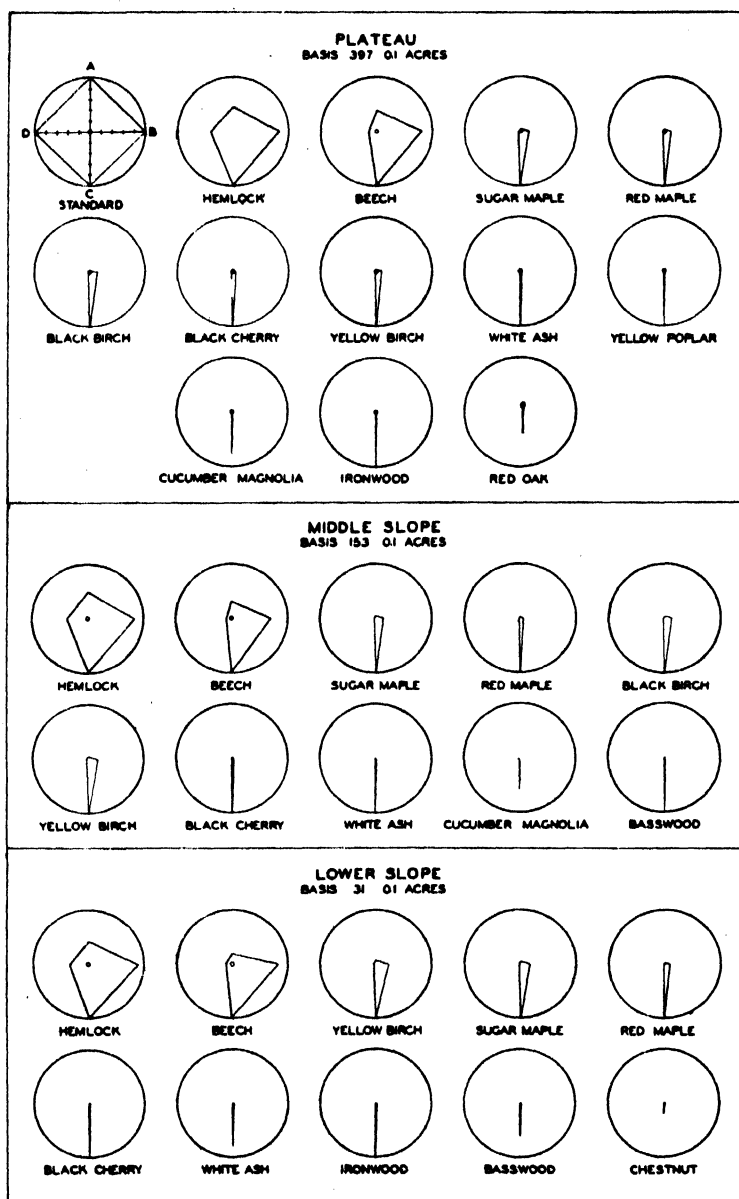


FIG. 3. Phytographs for principal dominant tree species on the plateau, middle slope, and lower slope of East Tinoesta.

On standard chart:

- O-A = Abundance in per cent based on total number of trees 10 in. d.b.h. and over (each division = 20 per cent).
- O-B = Frequency in per cent; a measure of the spatial distribution of a species based on occurrence of trees 10 in. d.b.h. and over on 1/10-acre plots (each division = 20 per cent).
- O-C = Number of size classes represented based on 5 divisions used by Lutz (each division = 1 size class).
- O-D = Basal area in square feet per acre for trees 10 in. d.b.h. and over (each division = 40 square feet). (Basal area is the cross sectional area of a tree bole in square feet, taken at breast height.)

nut, and basswood are the chief exceptions but are of very minor importance in the stand.

Neither the hemlock consociation nor the hemlock-beech association of Hearts Content has a species composition like that of the East Tionesta forest. The most striking difference in the dominant stand is the presence of white pine, red and white oak, and chestnut at Hearts Content and their rarity or absence at East Tionesta. Red maple is much more prominent and sugar maple of far less importance in the hemlock-beech association at Hearts Content than in any of the Tionesta samples.

Abundance and Frequency by Height Classes

Since the field tally included height as well as d.b.h. classes, it was possible to determine species composition (abundance), and distribution (frequency

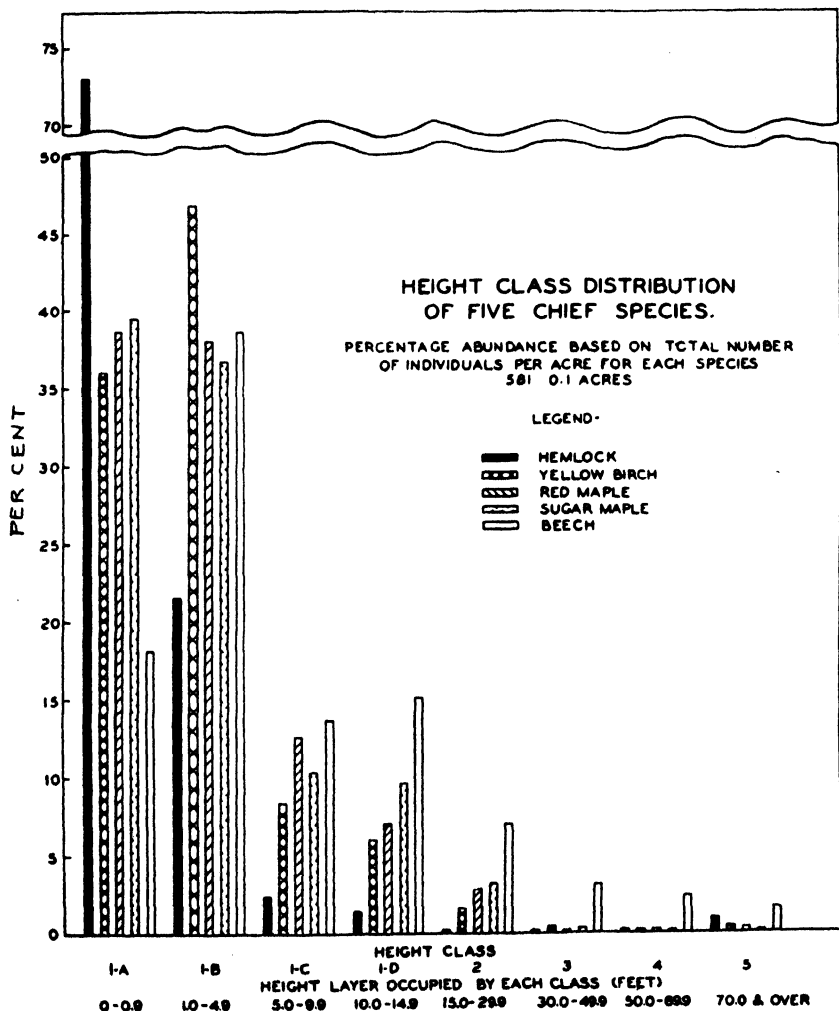


FIG. 4. Height class relationships within each of five chief species, based on entire sample of East Tionesta virgin forest.

of occurrence), for each of the five height classes. This indicates the extent to which species in the dominant tree class (height class 5), are perpetuating themselves in the intermediate heights down to small reproduction under 1 foot tall.

Tables I and II give the rank of the arborescent species, in abundance and frequency respectively, for each of five height classes. The species of greatest abundance or frequency is given a rating of 1. To obtain data for these tables and figure 4, all tallies of reproduction and larger trees were converted to a comparable per acre basis. Hemlock ranks first in both abundance and frequency among the dominant species (height class 5), on all topographic samples, while beech holds second place. The low rank of hemlock among trees between 5 and 30 feet tall is in striking contrast with the first or second rank held by beech in these height classes.

TABLE I. Rank of tree species according to abundance in eight height classes *

Species	Plateau								Middle slope								Lower slope							
	Height class								Height class								Height class							
	1				2	3	4	5	1				2	3	4	5	1				2	3	4	5
	a	b	c	d					a	b	c	d					a	b	c	d				
Beech.....	3	2	2	1	1	1	1	2	6	5	2	2	1	1	1	2	3	4	1	1	1	1	1	2
Hemlock.....	1	3	8	8	8	3	2	1	1	1	3	4	5	2	2	1	1	1	3	3	6	4	2	1
Sugar maple.....	2	1	1	2	2	2	3	4	2	2	1	1	2	3	4	4	2	2	2	2	5	4	4	4
Red maple.....	6	7	4	5	4	7	6	5	4	6	4	3	4	9	8	6	4	5	6	6	3	6	5	5
Yellow birch.....	4	6	6	7	7	5	7	6	3	3	5	5	3	6	3	3	3	3	4	4	3	3	3	3
Black birch.....	6	5	3	4	6	6	7	3	5	7	6	4	8	8	6	5	9	12		8		8		
White ash.....	8	10	9	9	9	7	4	8	8	9	10	8	6	7	5		9		7	8	7	7	7	6
Black cherry.....	7	8	7	6	5	4	5	7	7	10	9	9	7	4	6	7	7	14				2	5	
Hop hornbeam.....	11	12	11	10	11	7	8		9	11	12	10	10	5	7		8	13	10	9	8	5	6	
Blue beech.....								10	13	13	11	9	10				6	7	8	7	4	8		
Serviceberry.....	12	13															7	11	7	9	7			
Striped maple.....	5	4	5	3	3	5			6	8	8	7	7				10	8	9	8	7			
Mountain maple.....	10	9	10						6	4	7	6	12				5	6	9	5				
Witch hazel.....			13	11					13	11	9	6					10	10	5		5			
Basswood.....	13								12				11	10		8	15					6		6
Chestnut.....			13																		8			
Pin cherry.....																				9				
Cucumber magnolia..	9	11	12		12			10	10	12														
Yellow poplar.....	13	14	11	10	8	8	9																	
Bitternut hickory....						9																		
Red oak.....												12												

* Height classes recognized in East Tionesta study: 1a = 0-1 foot, 1b = 1-5 feet 1c = 5-10 feet, 1d = 10-15 feet, 2 = 15-30 feet, 3 = 30-50 feet, 4 = 50-70 feet, and 5 = 70 feet and over. Species within the same height class which had identical values for abundance were given the same rank.

In the absence of disturbing factors a tolerant species such as hemlock may be expected to build up an all-aged series of reproduction and young tree

sizes, due to the growth of established seedlings and current addition of countless newly germinated seedlings, a small percentage of which survive in favorable situations. Its evident failure to do so in East Tionesta may be logically ascribed to past factors unfavorable to the germination or survival of hemlock reproduction. Poor seed years, a severe drought period, porcupine damage,³ unfavorable soil conditions, and possibly ground fires, would ac-

TABLE II. *Rank of tree species according to frequency in eight height classes*

Species	Plateau								Middle slopes								Lower slopes							
	Height class								Height class								Height class							
	1				2	3	4	5	1				2	3	4	5	1				2	3	4	5
	a	b	c	d					a	b	c	d					a	b	c	d				
Beech.....	3	1	2	1	1	1	1	2	4	3	2	1	1	1	1	2	3	2	1	1	1	1	1	2
Hemlock.....	1	3	8	8	3	2	2	1	1	1	5	5	2	2	2	1	1	3	4	4	3	3	2	1
Sugar maple.....	2	2	1	2	2	3	3	4	2	2	1	2	3	3	4	4	2	3	2	2	2	4	3	3
Red maple.....	5	6	4	5	7	6	5	5	5	5	3	3	5	8	8	5	6	4	5	5	5	5	4	4
Yellow birch.....	7	8	7	7	6	5	7	6	3	4	4	3	4	4	3	3	4	1	3	3	4	2	2	3
Black birch.....	6	5	3	4	7	8	6	3	6	6	5	4	8	7	6	4	9	9	7	7	7	6	5	
White ash.....	9	9	9	9	8	9	4	8	9	10	9	8	6	8	5	8	5	5	7	7	7	7	5	
Black cherry.....	8	7	6	6	5	4	5	7	8	9	8	9	6	6	6	6	5	10	5	7	7	7	5	
Hop hornbeam.....	12	12	12	10	9	10	8	11	10	11	10	10	9	5	7		6	9	8	9	6	5	5	
Blue beech.....				12		12			11	13	12	11	7	9			5	7	7	6	5	7		
Serviceberry.....	13	13	14	11			11		13	13	12						5	7	8	6	9	7		
Striped maple.....	4	4	5	3	4	7	11		8	8	7	7	8				8	8	8	8	7			
Mountain maple.....	11	11	10	11					7	7	6	6	11				5	6	7					
Witch hazel.....			14	11					12	11	10	9					8	9	6	5	6			
Basswood.....	15	15		12		12	11		12	12			10	9	9	7	11					6	5	
Chestnut.....	15		13	11					14	13											7			
Pin cherry.....	14								12										9					
Cucumber magnolia.....	10	10	11	12	11	12	11	10	10	13						8								
Yellow poplar.....	14	14	13	11	10	11	9	9																
Bitternut hickory.....						10																		
Red oak.....	15						12					11												
Mountain ash.....	15	16							13	15														
N. white pine.....	15										15													
Mountain holly.....									15															
American elm.....									15			11												
Blue dogwood.....											12													

count for the lack of certain sizes. Information on this question is expected to result from an intensive study of the age history of this stand which was begun in 1934.

The relatively high rank held by yellow birch on the lower and middle slopes is interesting in view of its low rank (except in the 0-0.9 foot height class) on the plateau. This indicates similar conditions for germination and

³ Field records show porcupine damage on 40 per cent of all plots tallied, the greatest damage being done to beech, hemlock, black cherry, sugar maple, and yellow birch in the order mentioned.

ample sources of seed regardless of topography, but better survival in the larger height classes along slopes and stream bottoms.

Table II is in essential agreement with table I, that is in general a high abundance indicates a well distributed or frequent species.

Figure 4 illustrates graphically the number of individuals (in percentage of the total for that species), which occur in the various layers found in the East Tionesta forest. Naturally the tally of trees under 1 foot tall (Class 1 *a*) includes many newly germinated seedlings of the 1930 season, few of which may be expected to survive until next year. In the 1.0 to 4.9 foot height class may be found survivors of one or more seasons' annual crop of seedlings and sprouts. These are individuals of species best able to survive the rigors of the site because of inherent specific characteristics or accidents of location in a favorable position, such as an opening caused by a dead or windthrown tree. The severity of the struggle for existence faced by a small hemlock seedling in this forest is illustrated by the low percentage of individuals which have been able to survive and grow into the height classes over 5 feet tall. Out of a total of 7014 hemlock tallied per acre, 73 per cent or 5124 individuals were seedlings under 1.0 foot in height and only 1 per cent were trees over 70 feet tall. Computed on this basis the greatest number of individuals of hemlock, as of other chief species, are found in classes 1 *a*, *b*, and *c*, below 10 feet in height. Hemlock is, however, more abundant in dominant height class 5 than in classes 4, 3, or 2, as already stated in connection with table I. Beech is represented in all height classes, and, when even 1-foot intervals are used for trees under 10 feet tall, both beech and yellow birch are found to be more abundant in individuals under 1 foot tall than in any succeeding 1-foot class.

Diameter Distribution

A marked difference has been found between the diameter distribution graph of beech and hemlock in figure 5. Beech has a J-shaped graph for living trees 4" d.b.h. and over, while hemlock, especially on the plateau, tends toward a bimodal type of curve, due to a scarcity of trees between 4 and 7 inches d.b.h. This corroborates data presented in table I, reasons for which have been suggested. Tallies of recently dead hemlock on these same strips show a high mortality among trees of 4 and 5 inches d.b.h. Direct age counts are required to determine whether the hemlock is in an all-aged stand or is made up of even-aged groups (Hough, '32). The diameter distributions of other species resemble the J-shaped sugar maple graph but are of even less importance in the stand.

Mortality

The importance of windthrow as a destructive agent influencing the composition of this forest is shown by the tally of recently dead trees made on each 0.1 acre plot. Hemlock and beech are the chief windthrow sufferers, and of all dead trees 18 per cent resulted from windthrow. The surface soil

of this forest is marked by hollows and mounds formed by windthrown trees in the past. Certain limited areas, notably the height of land below Cherry Run, show severe wind damage which prostrated the dominant trees on a narrow strip during a single hurricane. A widespread blow-down during a single intense storm is probably less common than the loss of a single tree here

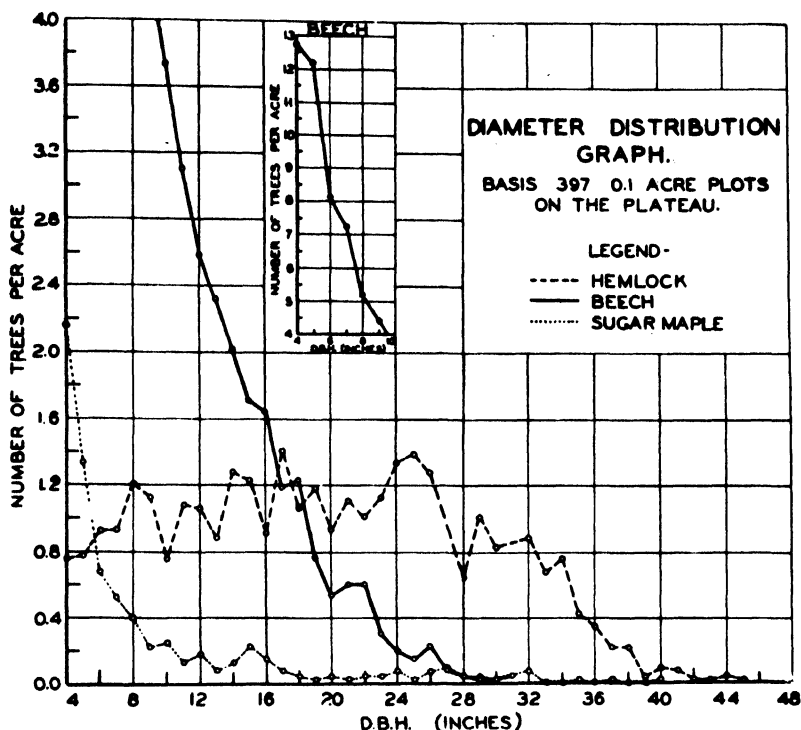


FIG. 5. Diameter distribution of three principal species on the plateau.

and there throughout the stand over a long period. Most of the dead trees tallied were killed by other causes than windthrow. Both hemlock and beech show peak mortality in the 4-5 and 4-6-inch d.b.h. classes respectively. Damage by porcupine has been suggested as a factor in the mortality of small trees. Hemlock losses are minor between 6 and 22 inches d.b.h. but the death rate then rapidly increases to a peak at 32 inches d.b.h. Mature trees of slow growth and reduced vigor are susceptible to drought, insect and fungus attacks, top girdling by porcupine, wind and snow break, windthrow, and other destructive agencies which cause natural decadence and mortality. The presence of intolerant species and their perpetuation in this virgin forest depends on opportunities presented by the mortality of dominant trees; examples are noted of sapling black cherry outstripping all competitors in small openings in the crown canopy.

Basal Area

An average basal area of 140.7 square feet per acre is found in this virgin forest. Hemlock is 63 per cent of the total basal area of dominant trees (10 inches d.b.h. and over), beech 20 per cent, sugar maple 4 per cent, red maple, black and yellow birch 3 per cent each, and other species are of minor importance. Among subdominant trees (3.6 to 9.5 inches d.b.h.), beech represents 70 per cent of the basal area, hemlock 12 per cent, sugar maple 5 per cent, yellow birch 3 per cent, and black cherry 2.5 per cent.

Shrubby and Herbaceous Vegetation

The vegetation of the forest floor, exclusive of arborescent reproduction, seldom exceeds 3 feet in height, *Viburnum alnifolium* and *V. acerifolium* being the largest perennial shrubby species. A layer ending at one foot above ground would include practically all herbaceous species; indeed the most common are trailing or rhizome-forming pteridophytes such as *Lycopodium lucidulum* and *Aspidium spinulosum* or have creeping underground rootstocks, such as *Oxalis acetosella*, *Mitchella repens*, and *Maianthemum canadense*.

In the enumeration of such species it was not always possible to be certain that each vegetative stem or clump of stems represented a separate individual plant or was attached to an extensive root system supporting many such stems. The practice of counting each clump of stems as an individual was followed in the case of trailing species. Stems of shrubby perennials such as *Viburnum*, *Lonicera*, *Sambucus*, *Rubus*, and *Ribes*, were counted as individuals, as were root suckers of beech and other tree species the underground origin of which could not be definitely determined. For this reason the frequency figures are probably more reliable than those of abundance.

A limited number of species were found exclusively in one topographic division of the area. These are not of sufficient abundance and frequency to have any indicator value for differences due to topography or soils. The habitat conditions for this forest floor vegetation are essentially similar whether under the plateau or lower slope forest. There is a reduction in the abundance and frequency of *Lycopodium lucidulum* in going from the plateau to lower slope. Some increase in *Tiarella cordifolia* and *Maianthemum canadense* occurs in the middle and lower slopes; these species are abundant in the adjacent second growth stands.

Common Plants

Lack of space forbids a comparison of the common plants of East Tionesta with those of Hearts Content (Lutz, '30). That the Tionesta forest is higher in the ecological scale of development than is the virgin white pine-hemlock-hardwood forest of Hearts Content, is indicated by the paucity of species reaching 5 per cent or over in abundance and 25 per cent or over in frequency. The dominant arboreal stand in particular is narrowed down to

hemlock and beech on the Tionesta plateau, with the addition of a relatively small amount of yellow birch on the middle and lower slopes. But four herbaceous and one shrubby species are common in both abundance and frequency in all topographic samples. It should be pointed out that *Aspidium spinulosum*, the most frequent herbaceous species in East Tionesta is likewise the most frequent at Hearts Content. Common species are starred in table III.

A study of the mosses and fungi of this area should be made. The most common fungus, saprophytic on hemlock logs, was found to be *Polyporus lucidus* (Leyss) Fries. Certain species of *Fomes* chiefly *F. applanatus* (Pers) Wallr, *F. fomentarius* (L.) Gill and *F. igniarius* (L.) Gill. on beech and *F. pinicola* (S.W.) Cooke on hemlock are important wood-rotting organisms.

Successional Relations

"Practically all of our forest trees go back farther than we can trace the warm blooded animals that furnished the stock out of which humanity arose in the late Tertiary, at about the time that the most luxuriant and widespread forests of the world were shrinking before those climatic changes that ushered in the glacial period and shattered their unbroken and far-flung distribution" Berry ('23). Postglacial evidence of forest conditions in Eastern North America has been obtained from counts of fossil pollen preserved in lakes and bogs from Iowa to Virginia. Sears ('35) sums up this evidence and concludes that, based on existing evidence and following the simple hypothesis of Von Post, postglacial time may be divided into three climatic periods: one of increasing warmth, one of maximum temperature, and one of slowly decreasing warmth.

We have no direct evidence of the antiquity of the East Tionesta flora but it is almost certain that some form of forest covered this non-glaciated area soon after the retreat of the ice sheet which lay about 25 miles to the northwest. The development of a residual podzolic soil indicates leaching under the acid duff of a prevailingly coniferous stand by a moist temperate climate. Direct age counts give a maximum age of 560 years for one specimen of hemlock the progenitor of which may have originated in a similar stand. Mature hemlock as old as 400 years were found growing on hummocks resulting from very old wind-throws of forest trees. A few mounds and hollows, nearly effaced by slow surface erosion, were beginning to assume the podzolized condition of adjacent undisturbed soil.

It might be expected that the composition or structure of this ancient forest would be different on the plateau, slopes, or valley bottom, due to differences in soils, climate, or biotic agencies. Assuming that an adequate sample of each situation has been secured, the "phytographs" of figure 3 show hemlock and beech, the two chief species of the dominant stand, to be remarkably uniform, despite the 500-foot range in altitude. An increase in

TABLE III (Continued)

Scientific name ⁵	Trees ¹	Common name	Per cent					
			Plateau based on 397 0.1 acres		Middle slope based on 153 0.1 acres		Lower slope based on 31 0.1 acres	
			Abun- dance	Fre- quency	Abun- dance	Fre- quency	Abun- dance	Fre- quency
Shrubby and herbaceous vegetation ³								
<i>Viburnum acerifolium</i>		Maple-leaved Viburnum	1.3	3	1.3	8	1.2	4
<i>Rubus allegheniensis</i>		Blackberry (bramble)	0.9	8	1.3	21	1.1	12
<i>Lycopodium obscurum</i>		Ground pine	0.8	3	1.0	4	0.1	3
<i>Impatiens</i> sp.		Jewelweed	0.8	1	0.3	1	0.6	1
<i>Polypodium vulgare</i>		Common polypody	0.6	1	1.0	5	0.7	2
<i>Arisaema triphyllum</i>		Jack-in-the-pulpit	0.5	7	1.0	14	0.2	10
<i>Medeola virginiana</i> ⁴		Indian cucumber-root	0.3	5	0.8	9	1.5	6
<i>Aralia nudicaulis</i>		Wild sarsaparilla	0.3	2	0.1	1	0.7	2
<i>Lonicera canadensis</i>		American fly honeysuckle	0.2	3	0.3	9	0.2	2
<i>Chrysosplenium americanum</i>		Golden saxifrage	0.2	1	0.3	9	0.3	4
<i>Dalibarda repens</i>		Dalibarda	0.1	2	0.8	4	0.1	3
<i>Brachyleytrum erectum</i>		Bearded short-husk	0.1	1	0.1	1	0.4	1
<i>Sambucus canadensis</i>		Common elder	0.1	4	0.2	1	0.1	3
" <i>racemosa</i>		Red-berried elder		1			0.1	
<i>Aspidium noveboracense</i>		New York fern	0.1	1	0.1	1	0.1	1
<i>Urtica</i> sp.		Nettle	0.1	1				
<i>Aclaea alba</i>		White baneberry		1				
<i>Pyrola elliptica</i>		Shin leaf		1				
<i>Pyrola americana</i>		American wintergreen			0.4	1	0.1	

¹ Only dominant trees, i.e. over 70 feet tall, considered.² Occur as dominant individuals on plateau but have very low values.³ Based on 290 milacre quadrats; 197 on the plateau, 77 on middle slope, and 16 on lower slope.⁴ Some *Trientalis americana* may be included through faulty field identification.⁵ Identifications of herbarium material were made by Dr. J. M. Fogg, Jr., of the University of Pennsylvania and by Dr. R. B. Gordon of Ohio State University. Identification of common species made by A. F. Hough.

* Common plant, 5 per cent or over in abundance and 25 per cent or over in frequency.

TABLE III (Continued)

Scientific name ⁵	Common name	Trees ¹							
		Plateau based on 397 0.1 acres		Middle slope based on 153 0.1 acres		Lower slope based on 31 0.1 acres		All based on 531 0.1 acres	
		Abun- dance	Fre- quency	Abun- dance	Fre- quency	Abun- dance	Fre- quency	Abun- dance	Fre- quency
Per cent									
<i>Ribes</i> sp.	Wild currant	1	0.2	4			0.1	1	
<i>Smilacina racemosa</i>	False solomon's seal	1						1	
<i>Trillium erectum</i>	Wake robin	1	0.1	1				1	
" <i>grandiflorum</i>	Large-flowered wake robin		0.1	3				1	
<i>Polystichum acrostichoides</i>	Christmas fern	1	0.5	5		6	0.2	2	
<i>Polygonatum biflorum</i>	Small Solomon's seal	1		1				1	
<i>Habenaria orbiculata</i>	Round-leaved orchis	1		3				1	
<i>Carex</i> sp.	Sedge	1	0.1	3				1	
<i>Gaultheria procumbens</i>	Wintergreen		0.2	4		6	0.2	2	
<i>Hepatica triloba</i>	Hepatica		2.8	4		6	1.0	1	
<i>Dicksonia punctilobula</i>	Hay-scented fern		1.6	6		19	0.7	3	
<i>Aster</i> sp.	Aster		0.3	1			0.1		
<i>Hydrophyllum virginianum</i>	Waterleaf		0.3	3		6	0.1	1	
<i>Scirpus</i> sp.	Club rush		0.2	3		13	0.1	1	
<i>Asarum canadense</i>	Wild ginger		0.2	3		6	0.1	1	
<i>Galium</i> sp.	Bedstraw		0.1	1					
<i>Waldsteinia fragarioides</i>	Barren strawberry		0.1	1		6	0.1	1	
<i>Agrimonia gryposepala</i>	Tall hairy agrimony		0.1	1		6	0.1		
<i>Allium</i> sp.	Wild onion		0.1	1		6			
<i>Dentaria diphylla</i>	Toothwort					6			
<i>Polygonum</i> sp.	Knotweed					6			
<i>Solidago rugosa</i>	Goldenrod					6			
<i>Caulophyllum thalictroides</i>	Blue cohosh					6			
<i>Lilium superbum</i> ⁶	Turk's cap lily					6			
<i>Epifagus virginiana</i>	Beech drops					6			
<i>Monotropa uniflora</i>	Indian pipe					6			
<i>Asplenium filix-femina</i>	Lady fern					6			
<i>Rudbeckia laciniata</i>	Tall cone flower					6			
<i>Mimulus ringens</i>	Monkey flower					6			
<i>Scutellaria lateriflora</i>	Mad-dog skullcap					6			

⁶ Last 7 species were found on the area but not encountered on the measured quadrats; they are of low abundance and frequency.

yellow birch along the East Tionesta creek bottom (lower slope) is the chief difference in composition which may be linked with site factors. Accepting the idea that this forest is a climatic climax association, how can decadence of dominant trees and wind-throw, be reconciled with the idea of a stable climatic climax? As pointed out by Tansley and Chipp ('26) all that can be claimed is that a climax type is relatively permanent under the given conditions. The criterion of stability appears to be ability to perpetuate itself in essentially the same floristic and ecological structure as long as the climatic, biotic, and physiographic conditions remain unchanged.

Destructive agencies have placed their mark on the East Tionesta forest and its present ecological structure reflects the result of this struggle with its environment. The forest has all but effaced some of these past disturbances, while others are comparatively fresh and offer an opportunity to study the steps by which such catastrophes are repaired. The amount of recent severe climatic or biotic disturbance is limited to a small percentage of the entire sample on which this study is based. Such local areas are included with the bulk of undisturbed forest in this analysis since no defensible criteria for their elimination could be seen. (No plots were taken in man-made oil or gas well openings, pipe lines, or trails, and recent disturbance due to logging was avoided.) Wind damage and mortality from other causes have been in operation for a period much longer than the maximum age of living trees. There is no reason to believe that these factors are any more active or effective in changing the composition of the stand today than they were in the past. Openings in the crown canopy are not widespread as a rule; severe windstorms during the life of the present trees have disturbed little of the area studied. Other destructive agencies such as the severe drought of 1930 followed by the eastern hemlock borer, *Melanophila fulvoguttata* Harr., create openings in which secondary successions may begin.

The influence of these openings on the perpetuation of less tolerant species than beech and hemlock has been recognized. It is evident that intolerant species such as black cherry, cucumber magnolia, yellow poplar, basswood and white ash, are minor components of this virgin forest. These species exist by virtue of superior initial growth rates which enable them to secure dominance in openings made by mortality of the overwood. Only severe blow-down, fire, insect attacks, logging, or some other major catastrophe can bring in these species in abundance.

SILVICAL CHARACTERISTICS

The silvical characteristics of tree species found in East Tionesta suggest reasons for the high rank of beech and the persistence of hemlock in this forest community. Beech, the major hardwood species, owes its prominence in the stand partly to its ability to reproduce by root suckers as well as by seed. Ability of these root suckers to stand severe droughts and root competition is coupled with the longevity of parent trees from which they receive

nourishment and water. Seedling beech which once become established are also very tolerant. Understory beech is both abundant and frequent, and is found on areas dominated by both hardwoods and hemlock. Destruction of the dominant stand thus tends to favor the beech already present on the site, unless rapid growing competitors also happen to be present. Beech, like its associate hemlock, is able to stand suppression and make slow growth for years with no apparent lessening of vigor, and, after 100 or more years is still able to put on rapid growth if released from nearby competitors.

Of most importance in the survival of hemlock is thought to be its great life span and extreme tolerance. Hemlock, according to Marshall ('27) retains the ability to grow vigorously after long periods of suppression and may be regarded as physiologically young though of great actual age. The Experiment Station has found on sample plots in Warren County, Pennsylvania, that hemlock suppressed for 130 to 304 years, with stump diameters of 7 to 16 inches, had made rapid diameter growth when released by cutting. With this great advantage of ability to endure long periods of suppression and yet respond to better growing conditions, and with a maximum life span of over 500 years, hemlock can outlast the hardwoods, awaiting their decadence and supplanting them individually or in groups. Had the tendency been otherwise and the hardwood species retained their ascendancy over hemlock during a long period in the past there would not be the great abundance of hemlock in the dominant tree class that we find today.

The habits of reproduction of hemlock also offer a reason for its presence in this forest. Hemlock seedlings germinate on rotted wood of all species where they seem to survive better than on the forest floor. Since the majority of large down logs are hemlock, it may be said to grow on the "bones" of its ancestors. Mortality of an old tree thus seems to guarantee the growth of a large number of hemlock seedlings and, while their development may be very slow, it is inevitable that a few of the many which start will survive to maturity.

It is possible that factors unfavorable to the regeneration of hemlock have come into the East Tionesta since the white man settled Pennsylvania. Extirmination of the bob-cat and cougar, which were practically the only enemies of the porcupine, may well have created an over-population of this tree destroyer, dangerous to tender-barked hemlock saplings.

A silvical characteristic of hemlock which ties in directly with damage caused by windthrow is its habit of shallow rooting. During the spring months, when the soil is thawed out and full of water from melting snow, high winds are apt to uproot tall veteran hemlock. One tree may fall against others, and aid in uprooting them, to form a considerable opening, the regeneration of which is usually accomplished by hardwood species. Thus hemlock and hardwoods probably alternate in the occupation of a given spot.

Of the less abundant hardwoods in East Tionesta, sugar maple has reproduced almost as well as beech and outranks yellow birch. Ability to ger-

minate on leaf litter, and survival of tolerant seedlings, is characteristic of the maples.

Yellow birch is a common species on the middle and lower slopes, reproducing readily on moss covered rocks and on old logs. With its light wind-borne seed, yellow birch is widely distributed and by reason of its growth on upturned soil and rotted logs is especially prominent after wind-throw of the old stand. The seedlings seem able to endure a moderate amount of shade though not as tolerant as hemlock or beech.

SUMMARY

The East Tionesta tract is the largest remnant of original forest now standing in Pennsylvania. A study of 1200 acres of this forest was made by the Allegheny Forest Experiment Station in 1930.

Out of 651 plots of 0.1 acre each, a total of 587 were used as a sample of unburned and uncut virgin forest. These were divided on the basis of topography (because no essential compositional differences could be noted) into 397 plots on the plateau, 159 plots on the middle slopes, and 31 plots on the lower slope. The shrubby and herbaceous vegetation was studied on 290 staked milacre quadrats.

For classification of the arborescent vegetation five height classes or layers of tree crowns were recognized. The dominant stand (trees 70 feet and over in height) is made up almost entirely of hemlock and beech with small percentages of sugar maple, yellow birch, red maple, black birch, black cherry and others. Compared to Hearts Content the absence of white pine is significant, and the East Tionesta forest represents a more advanced ecological stage believed to be the climatic climax of the region.

The species composition of the dominant stand and reproduction has been studied for evidence of the factors which have operated to produce and perpetuate this hemlock-beech association. Absence of fire in the area studied is an important factor. Openings caused by climatic and biotic agencies have been suggested as factors allowing the entrance of intolerant species into the climax association and also influencing the mortality of hemlock and its replacement by hardwood species.

Reproductive habits and growth requirements of beech, hemlock, yellow birch, and the maples have suggested reasons for the high rank of beech and the persistence of hemlock in this forest.

On certain sites the hardwood species seem to have dominated the stand for long periods of time while elsewhere hemlock is now dominant, and, on certain stream bottom sites, gives promise of perpetuating itself indefinitely almost to the exclusion of hardwood species.

Such areas are localized and usually of small size; the characteristic composition seems to be a forest in which hemlock and beech grow side by side and may both be represented in the dominant height class.

Further studies are needed to present a complete picture of the age relationships of species but available evidence now points to the climatic climax nature of this East Tionesta hemlock-beech association. Dominance of hemlock and beech in this association has been the result of natural selection under the prevailing climate, soil, and animal population of the area.

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EROSION SILT AS A FACTOR IN AQUATIC ENVIRONMENTS¹

M. M. ELLIS

Interior Fisheries Investigations, U. S. Bureau of Fisheries

The increasing loss of surface soil by erosion during the past few decades has been pointed out by various writers on soil and forestry problems (Bennett and Chapline, '28; Bates and Zeasman, '30; Bailey, Forshing and Becraft, '34), and because of this rapid, uncontrolled erosion progressively larger amounts of erosion silt are being contributed to the fresh water streams by floods, dust storms and surface run-off. These enormous loads of erosion silt (429 million tons for Mississippi River, Bennett and Chapline, '28), have already produced at numerous points marked changes in both the aquatic habitats and biota of many streams, and have changed their waters from clear to muddy for all or a greater part of the year. In order to ascertain quantitatively some of the specific effects of erosion silt on aquatic complexes, biophysical and biochemical studies have been made at over 700 stations on streams of the Mississippi-Ohio-Missouri System, and other interior waters. These field observations have been supplemented with experimental work at the Bureau of Fisheries Laboratories at Columbia, Missouri and Ft. Worth, Texas.

Erosion material added to the waters of any stream has two major contacts with the living organisms in that stream, first through the aqueous medium because of the physical and chemical changes which the erosion silt produces in the waters themselves, and second, through alterations in bottom conditions resulting from the subsequent settling out of all or part of the silt load. The data presented have been grouped accordingly.

LIGHT PENETRATION INTO WATER CARRYING EROSION SILT

As a routine procedure all water samples were first filtered through bolting cloth to remove plankton organisms and bits of debris. Direct measurements of the turbidity of the water carrying erosion silt were then made with a photoelectric apparatus (Ellis, '34), which gave values similar to those obtained by comparison with standard suspensions (U. S. G. S. turbidity units), and by the Secchi method (Standard Water Analysis, '33). However, as these turbidity values are merely statements of relative opacity, and as the readings from the photoelectric apparatus are readily convertible into light penetration values (see Ellis, '34), the depth in millimeters of water of the given turbidity required to screen out 99.9999 percent of the light entering

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at the surface, *i.e.*, the depth at which light would be reduced to one-millionth of its surface intensity, was chosen as a measure of the light screening power of the various waters studied. This depth is subsequently referred to as the "millionth intensity depth," or "m.i.d."

Limits of Penetration of Visible Light into Waters Carrying Erosion Silt

Excepting surface run-off immediately after heavy rains, the maximum opacity determined for muddy water from natural streams was that of a sample from the Missouri River collected near the surface at Boonville, Missouri, November 23, 1931. The millionth intensity depth of that water was only 84 mm. The clearest natural stream water (not springs) was taken from the Rio Saltillo, near Saltillo, Estado Coahuila, Mexico, a little mountain stream flowing over a rocky bottom and at the time carrying practically no erosion material. The millionth intensity depth for this stream was 53,887 mm. or roughly 53.9 meters. These two values, 84 and 53,887 mms., the extremes found in over 5,000 determinations of the m.i.d. of inland waters of the United States and northern Mexico, will serve to establish the general range of m.i.d. in interior waters varying from a very muddy river to a clear mountain stream.

However, as mountain streams are characteristically very clear the millionth intensity depths of waters from clear streams in central United States flowing through relatively undisturbed wooded or swampy areas which might be considered as fairly representative of conditions before uncontrolled erosion began, were determined for comparison with mountain streams like the Rio Saltillo, and with muddy rivers like the Missouri. A few examples will suffice. Portions of the Niangua River drain a sparsely settled area in the hilly Ozark country of Missouri, where limestone outcrops are numerous and where the land is covered by a good growth of scrub oak. The millionth intensity depth for clear water from this stream ranged from 11,000 mm. to 20,000 mm. The St. Francis River drains the cypress swamp district of southeastern Missouri and northeastern Arkansas and for small tributaries of this stream, flowing out of uncultivated swampy areas the m.i.d. was between 11,000 mm. and 12,000 mm. Similar degrees of clearness were found even in the Ohio and Tennessee Rivers during very low water when these rivers were receiving the minimum amount of erosion material. During the month of July, 1931, intensity depths from 4,000 mm. to 17,000 mm. were typical for the Ohio River between Cairo, Illinois and Paducah, Kentucky and from 4,700 mm. to 20,000 mm., for the Tennessee River at Paducah, Kentucky. However, when rain came the turbidity of the Tennessee River rose due to the erosion silt load, and the m.i.d. fell to less than 200 mm. in 48 hours. In contrast to this change in the Tennessee River following rain, the Sturgeon River in Baraga County, Michigan, draining a swampy woodland area had a m.i.d. of 6,000 mm. after a three day rain (August, 1934).

Collectively the data from unpolluted portions of inland streams in areas naturally protected against undue erosion showed that a clearness of water permitting light penetration 10,000 mm. to 20,000 mm. before the millionth intensity depth was reached, was maintained most of the time, and that even following unusual rains the erosion material rarely reduced the m.i.d. of streams in these protected areas below 6,000 mm. These values are in sharp contrast with those found for waters from streams receiving quantities of erosion silt.

Above Grand Rapids, Minnesota, in the unpolluted headwaters of the Mississippi which drain a swampy lake region, in protected portions of the St. Croix River, north of Hudson, Wisconsin, and in some of the small tributaries of the upper Mississippi, as the Zumbro which flows out of grassland dairy country, millionth intensity depths ranging from 6,000 mm. to 34,400 mm. were found consistently under existing conditions (1934), *i.e.* in general the headwaters of the Mississippi River, where protected from erosion silt and pollution, were of a clearness comparable to streams like the Niangua and the tributaries of the St. Francis, as previously discussed. Pollution from the Twin Cities reduces the m.i.d. of the Mississippi to around 2,000 mm. in the lower part of the Hastings Pool near Hastings, Minnesota, but the m.i.d. rises to between 4,000 mm. and 6,000 mm. at the foot of Lake Pepin. These reductions in m.i.d. as compared with the m.i.d. of the headwaters are due largely to organic matter in solution rather than to erosion silt.

Below the mouth of the Chippewa River, near Reeds Landing, Minnesota the additions of erosion material become progressively more evident, and at Alma, Wisconsin readings as small as 1,500 mm. were not unusual even during "clear water" periods. South of Alma, Wisconsin the average m.i.d. fell rapidly to 1,000 mm. or less due to the erosion load and sudden fluctuations became common. At Clayton, Iowa, on July 27 the m.i.d. was 1,209 mm. and 24 hours later at DeSoto, Wisconsin, it was 115 mm. following a heavy storm on Root River. During the summer of 1934, the m.i.d. for Mississippi above Lock 15 at Davenport, Iowa, varied from 1,854 mm. to 123 mm. with an average of 466 mm. Similarly of 392 samples from the Mississippi between Davenport, Iowa and Grafton, Illinois (May 22 to September 9, 1932), 87 per cent had a m.i.d. of less than 330 mm. with a maximum of 2,000 mm. Near St. Louis, Missouri, the Mississippi after receiving the Missouri River but before receiving the sewage and wastes of the City of St. Louis, had (September, 1934) a m.i.d. of less than 200 mm., while at Cairo, Illinois, Memphis, Tennessee, Greenville, Mississippi and New Orleans, Louisiana, the m.i.d. was consistently less than 175 mm. and for many samples smaller than 150 mm. The addition of the waters of the Missouri River complicates the determinations of the effects of erosion silt on light penetration into the waters of the lower Mississippi because the Missouri River was known as a muddy river even before the white man took over Kansas, Nebraska, and the Dakota as the natural erosion in the upper Yellowstone region

has long been severe. However, the present erosion silt loads due to uncontrolled erosion for which man is largely responsible have reduced the m.i.d. of the Upper Mississippi, *i.e.*, the Mississippi above the mouth of the Missouri, from a range between 6,000 and 20,000 mm. to one between 150 and 2,000 mm. with the average less than 300 mm.

Similar changes have taken place in the Tennessee River which many river pilots living today remember 20 to 25 years ago as a relatively clear stream even after heavy rains. July 20 to August 30, 1932, the writer examined 496 samples from the Tennessee River between Paducah, Kentucky and Hiwassee Creek above Chattanooga, Tennessee. The millionth intensity depth for these samples averaged 1,000 mm. with 42 per cent of the samples less than 350 mm. although the river was low and rains few, yet at Paducah, Kentucky as has already been pointed out this river during very low water frequently had a m.i.d. of 20,000 mm.

As these enormous changes in light penetration depths charged to erosion silt might be due in part to substances in solution many samples from typical localities were forced through a colloidal filter (Whatman No. 40 filter paper filled with celloidin) under 80 pounds pressure. This procedure gave sparkling clear filtrates containing the dissolved substances and the light transmission through the filtrate was compared with that through the original unfiltered water. The millionth intensity depths of both filtered and unfiltered samples are given for a few river waters of high turbidity, as typical; Mississippi River, Keokuk, Iowa, unfiltered 235 mm., filtered 34,000 mm.; Mississippi, Memphis, Tennessee, 188 mm., 8,000 mm.; Missouri River, Boonville, Missouri, 115 mm., 8000 mm.; Black Warrior River, Demopolis Alabama, 645 mm., 17,104 mm.; Tombigbee River near Tuscaloosa, Alabama, 323 mm., 6,869 mm.; and Mobile River near Mt. Vernon, Alabama, 764 mm., 68,800 mm. It may be seen from these figures that, freed of the erosion silt, the waters of these very muddy rivers were of a clearness comparable to that of the clear streams from protected areas, *i.e.*, the erosion silt load had not changed the amount of natural organic detritus carried by the stream, nor increased to any extent the quantities of dissolved substances interfering with the transmission of light. Any rise in dissolved colored substances in river waters was found primarily as the result of introduction of organic wastes, as in Hastings Pool and Lake Pepin, where the organic pollution from the Twin Cities gave the water a distinct brownish color.

As the significance of the millionth intensity depth in showing the screening out of light by erosion silt in river water, depends upon a maintained and relatively uniform turbidity from surface to bottom as great as that of the sample, whenever possible m.i.d. determinations were made on water from different depths, supplemented with measurements of the rate of clearing due to the settling out of the silt. From several thousand m.i.d. readings at various depths two statements may be made. First, the vertical distribution of erosion silt, after the scourings and heavier particles of sand are removed,

is fairly uniform in the water of flowing rivers with a tendency toward increased turbidity near the bottom in the slower parts of the stream; and second, in impounded waters back of power dams if the water be deep enough and the current slow enough to allow thermal stratification in summer, there is a marked stratification of erosion silt in the deeper waters.

Readings every 12 hours together with various readings at all hours of the night and day on the m.i.d. of Lake Keokuk, Mississippi River, from samples at the surface (0.5 meter) and bottom (8.5 meters) levels for 40 consecutive days (July and August, 1932) involving over 340 observations show that the suspended silt is quite uniformly distributed at all times throughout this body of water, which has a current of 3 to 4 miles per hour, a maximum depth of approximately 9 meters, and no thermocline. During period mentioned the m.i.d. varied from 88 mm. to 1,548 mm., with 47 per cent of the surface readings and 54 per cent of the bottom readings less than 380 mm. Even the deep holes of rivers showed this rather uniform distribution of the suspensoids. Off Tower Rock near Grand Tower, Illinois the surface m.i.d. of the Mississippi River on September 8, 1931, was 129 mm., decreased progressively to 119 mm. at the 30 meter level and rose to 124 mm. at the bottom, 33 meters. At Pan Eddy in the Tennessee River on August 31, 1931, the surface m.i.d. was 548 mm., and decreased gradually to 500 mm. at 39 meters, the bottom. No thermal stratification of water was found either at Tower Rock or Pan Eddy.

In various of the deeper power dam lakes, created by impounding rivers, as Lake Wilson, Tennessee River, and Lake of Ozarks, Osage River, a very definite stratification of the erosion silt load however was observed. In these river lakes stream flow and depth are such that during the summer months there is definite thermal stratification of the water, with a well defined thermocline. In Lake Wilson during July and August extending from the surface to approximately the 18 meter level there is an upper mass of water in which the temperature declines gradually as the depth increases. This mass of water, the hyperlimnorrheum, flows steadily downstream. Below the hyperlimnorrheum is second mass of water between the 18th and 21st meter levels, a true thermocline in which the temperature of the water drops abruptly. The water in the thermocline zone does not flow appreciably. A third mass of water extends below the thermocline, *i.e.*, from approximately the 21st meter level to the bottom of the lake. This mass of water is quiet during the summer and is a true hypolimnion. A set of m.i.d. determinations at Sta. 385 in Lake Wilson on August 24, 1931, will suffice to show the vertical distribution of silt in these three masses of water. The surface m.i.d. on that day was 1,147 mm., decreased progressively to 1,070 mm. at the 15 meter level, and rose to 1,127 mm. at the 18 meter level, the bottom of the hyperlimnorrheum. At the 21st meter level, the lower limit of the thermocline, the water had cleared so that the m.i.d. was 4,143 mm. and from the 24th meter level to the bottom, 33 meters, the water was sparkling clear with

a m.i.d. of 7,860 mm. The abrupt change in water temperature and correlated change in water viscosity in the thermocline produced this stratification, so that during the warm summer months in several of these deep power dam lakes the writer has found a warm muddy river, the hyperlimnorrheum, flowing over a cold, clear lake, the hypolimnion, with very little mixing in the thermocline.

Settling out studies of river waters carrying various quantities of erosion silt showed that with the exception of the scourings, *i.e.*, the heavy particles of sand found particularly in water where the current was swift, the finer erosion material remained suspended for hours even in water which was undisturbed, *i.e.*, the m.i.d. was still greatly reduced by the erosion silt after 48 to 96 hours settling. As settling out curves have been plotted for various river waters by hydrographic engineers, the rates of settling need not be discussed here, but the present studies have brought out the fact that the very fine suspensoids, *i.e.* those which are the last to settle out and therefore those which would remain suspended were the water subject to even slight agitation, are very effective in screening out light in river water. A detailed case of the clearing of water by settling and the corresponding rise in the m.i.d. may be taken as typical of several hundred determinations of this sort. At Pharrs Island, near Clarksville, Missouri, the surface m.i.d. of the Mississippi River water on August 24, 1932 was 157 mm. After standing 1 hour the m.i.d. rose to 176 mm.; after 2½ hours to 221 mm.; after 20 hours to 421 mm.; after 48 hours to 1,009 mm.; and after 96 hours to 1,639 mm. The silt still remaining therefore at the end of 20 hours settling reduced the m.i.d. of the water (as shown by filtration samples) from 15,000 mm. to 421 mm. and at the end of 96 hours to 1,639 mm., *i.e.*, even after 96 hours of undisturbed settling, a condition which would rarely occur in the river, the silt load reduced the light entering the surface of the water to one-millionth of its surface intensity in approximately the first 1.5 meters as compared with 15 meters for this same water without its silt load. In many cases the colloidal clays carried by inland stream waters maintained effective screens against light penetration for even longer periods than in this average sample from the Mississippi River. These suspensions, however, could be quickly discharged by adjusting the water to a pH of 8.8 to 9.1, an alkaline condition not found in normal river water.

Penetration of Colored Light of Various Wave Lengths into Waters Carrying Erosion Silt

As the physiological and biological effects of light vary with the wave length, the selective action of erosion silt against light entering river water was studied both by spectrographic photographs of light transmitted through waters carrying erosion suspensoids and by the measurements of the transmission of colored light through such samples, as recorded by the photo-

electric apparatus. In both cases the light transmission of each of the various pieces of glass apparatus and screens (Corning Glass for colors) was standardized spectrographically against the helium spectrum as photographed on the same plate.

Selective penetration studies showed that waters carrying large loads of erosion silt transmitted in general more red light than light of the shorter wave lengths, with a maximum transmission in the scarlet-orange zone, *i.e.*, light of wave lengths between 6,600 and 5,850 A. U. However this differential in favor of the red rays was not large, especially in less turbid waters, so that the major effect of the suspended erosion silt is that of an opaque screen, regardless of the color of the light. The high selectivity of clear ocean water and distilled water favoring the transmission of light between 4,700 and 5,500 A. U., the bluish and yellowish greens (Shelford, '29; Pietenpol, '18), was not found in water carrying even a small amount of erosion silt. In fact some muddy waters, possibly as the result of dissolved substances, seemed slightly selective against the blue green light. The various findings on the penetration of colored light into river waters containing erosion silt were checked and verified by studies of light penetration through prepared suspensions in distilled water of white adobe clay, red clay and black humus and through similar suspensions of muds dredged from the bottoms of Lake Wilson, Lake Keokuk and Lake Pepin at points where extensive deposits of erosion silts were found. These tests showed that the color of the soil was practically a negligible factor, in determining the color of light transmitted through waters containing erosion silt, except for possibly a small amount of selective reflection of light from the silt particles in very dilute suspensions. The erosion silt particles, therefore, screen out the light very largely as opaque objects regardless of their own individual color.

Spectrographic photographs of light transmitted through river water carrying erosion silt confirmed the findings on light penetration into such waters as stated above. Figure I gives spectrographic photographs of Missouri River water before and after filtering and of unfiltered water from the Hinkson River, a small Missouri stream flowing over a limestone bed but through farm land. These photographs show a differential in favor of the red end of the spectrum.

TEMPERATURE ADJUSTMENT OF SILT-LADEN WATER

The heating and cooling rates of water carrying erosion silt as compared with distilled water was determined for various samples in standardized two-liter pyrex flasks immersed in electrically controlled constant temperature water baths. When desired the fluid inside the flask was kept in motion by a motor driven glass stirrer making approximately 150 r.p.m. The data from these heating and cooling tests, when expressed graphically gave curves for the rates of heat transmission and heat radiation in waters carrying ero-



3889

4472

4927 4713
5016

5876

7065 A.U.
6678

Description of figure 1 on opposite page.

FIG. 1.

sion silt that were essentially the same as those for distilled water (with of course a slight allowance for the small amounts of electrolytes present in the river waters) if the water samples were constantly and sufficiently agitated. However, if the samples were undisturbed the stratification of the erosion silt particles as they began to settle out or otherwise re-

TABLE I. *Cooling and heating of water from Coal Creek, near LaFollette, Tennessee, April 25, 1934*

Minutes after immersion	Distilled water in degrees C.	Unagitated		Agitated	
		Coal Creek		Distilled water in degrees C.	Coal Creek unfiltered ² in degrees C.
		Filtered ² in degrees C.	Unfiltered ² in degrees C.		
start	19.7	19.7	19.7	37.0	37.0
2	22.8	22.8	22.0	35.0	35.0
4	26.6	26.6	25.2	32.0	31.9
6	29.5	29.4	28.0	30.2	30.0
8	31.5	31.5	29.7	29.0	28.8
10	33.0	32.9	31.2	28.0	28.0
12	34.0	34.0	32.3	27.4	27.4
14	34.8	34.7	33.0	26.9	27.0
16	35.4	35.3	33.7	26.5	26.6
18	35.9	35.8	34.2	26.2	26.3
20	36.2	36.2	34.6	25.9	26.0
22	36.4	36.3	35.0	25.8	25.8
24	36.6	36.6	35.3	25.6	25.6
26	36.7	36.7	35.6	25.4	25.5
28	36.8	36.8	35.8	25.4	25.4
30	36.9	36.9	36.0	25.3	25.3
40	37.0	37.0	36.5	25.3	25.3
		Bath temperature 37°C.		Bath temperature 20° C.	

² m.i.d. 614 mm. as taken from stream.

³ m.i.d. 17,000 mm. after passing through colloidal filter.

arrange themselves definitely interfered with heat transmission and produced a skew lag in both the warming and cooling curves of waters carrying erosion silt as compared with distilled water. Temperature affects the metabolism of aquatic organisms and alters various physical and chemical factors,

FIG. 1. Spectrographic photograph showing light transmitted through water carrying erosion silt.

A = Helium spectrum. The wave lengths of the more conspicuous lines are given in Angstrom Units at bottom of figure. 1 minute exposure.

B = Hinkson River water, unfiltered. Sample taken near Columbia, Missouri, November 23, 1931, m.i.d. 1,846 mm. 30 seconds exposure.

C = Open light. 30 seconds exposure.

D = Empty flask. 30 seconds exposure.

E = Missouri River water, unfiltered. Sample taken near Boonville, Missouri, November 23, 1931, m.i.d. 84 mm. 20 minutes exposure, sample shaken every 2 minutes to maintain complete suspension.

F = Missouri River water, filtered. Same sample as "E," after passing through colloidal filter, m.i.d. 8,000 mm. 30 seconds exposure.

as dissolved oxygen, in the waters of the stream, so there are several applications of the findings from these heating and cooling tests, particularly to river lakes. As has already been pointed out in the larger river lakes as Lake Wilson, during the summer there is a large band of warm water, the hyperlimnorrheum, carrying the silt load of the river, and flowing on top of the clear cold water of the hypolimnion. The blanket of silt carried by the hyperlimnorrheum in view of these heating and cooling data, must alter the rate of heat exchange between the surface waters and those in the deeper parts of these river lakes. In table I a typical set of these data from studies of samples from Coal Creek, a small tributary of the Clinch River near La-Follette, Tennessee, are presented.

EROSION SILT AND THE ELECTROLYTES OF RIVER WATERS

As has been pointed out under the discussion of light penetration into waters carrying erosion silt, the amounts of soluble substances in the filtrates after passing river waters through colloidal filters were small, and bore no very definite relation to the amount of erosion material present in the original sample. Variations in the amounts of soluble, colorless substances determined either as electrolytes by means of a standard specific conductance cell containing platinum electrodes and operating with a micro-hummer and telephone receiver, or specifically by the various analytical procedures as amounts of the salt were also independent of the erosion silt. The work on electrolytes in connection with erosion silt may be summarized quite briefly therefore although the electrolytes were frequently of much importance in stream pollution studies. The average specific conductance of relatively unpolluted river waters carrying erosion silt varied from 388 to 133 mho at 25° C.,² the usual value for the larger streams being near 290 mho, and the conductance of the whole river water, *i.e.*, river water carrying erosion silt was essentially the same as the conductance of the same sample of water after the erosion silt was removed by a colloidal filter. After sudden heavy rains the specific conductance of the river water usually fell, and never increased although the erosion silt load and consequently the turbidity rose greatly. These observations indicate that, under the existing conditions of erosion, rains and high waters add proportionately more insoluble material (erosion silt) than soluble electrolytes. Consequently following rains or high waters the available mineral salts in the water and the light penetration are both reduced in the river lakes as Lake Keokuk, Lake Pepin and Lake Wilson. A definitely correlated decrease in the plankton per unit volume of the water was noted at such times.

In connection with the salt complex of river water it may be noted that the erosion silt particles in most river waters were quickly discharged and precipitated when the pH of the surrounding water was adjusted to 8.8 to

² These values are times 10^{-4} .

9.1, and that the erosion silt was found to have a slight buffer value against acids, particularly in regions where there were limestone outcrops.

EROSION SILT AS AFFECTING BOTTOM CONDITIONS

Blanketing of Stream Bottom

The effects of rapid blanketing of stream bottoms by layers of silt which smother out the existing fauna before it can readjust are well known. The sedentary biota suffers particularly during these sudden inundations of erosion material following floods and high waters, although many of the mobile species are affected either directly or indirectly through the loss of food supplies. The magnitude of some of the silt deposits and their effects on fisheries and fresh-water mussels in the Mississippi and Tennessee systems have already been discussed (Ellis, '31 a and b). However to determine the specific effects of slowly deposited silt under controlled conditions over 2,000 fresh-water mussels representing 18 of the common species were carried in a set of experiments conducted in the raceways at the U. S. B. F. Station at Ft. Worth, Texas. Special bottoms of measured sand or gravel were laid in these raceways and optimum conditions for mussels established at the start. Above these prepared bottoms wooden lattice-work trays were constructed so that mussels could be held at various levels in the same water, subject to the same silt deposits as the mussels in the gravel or sand at the bottom of the raceway, except that silt could not accumulate around or over the mussels in the trays. The raceways were supplied with running water from Lake Worth, an unpolluted, impounded portion of the Trinity River which carries a moderate load of very fine erosion silt, chiefly adobe clay with very little organic matter. The average turbidity of the water in the raceways represented a m.i.d. of 800 to 1,200 mm., i.e., the water was not overloaded with silt. The current in the raceways was reduced so that conditions of silting comparable to those in the quieter portions of normal streams were maintained. The individual mussels were marked and the entire series inspected once or twice weekly.

These experiments, extending over some fourteen months, showed that most of the common fresh-water mussels were unable to maintain themselves in either sand or gravel bottoms when a layer of silt from one-fourth of an inch to one inch deep was allowed to accumulate on the surface of these otherwise satisfactory bottom habitats, although other individuals of these same species held in the lattice-work crates a few inches or feet above the bottom thrived in this same water. Daily analyses of the water at various levels in these raceways showed that the high mortality of the mussels on the bottom was induced by the silt covering and was not due to low oxygen, pH, carbonates or other water conditions. The Yellow Sand-shell, *Lampsilis teres*, a sand inhabiting species was the most readily killed by silt deposits, and the Three-horned Warty-back, *Obliquaria reflexa*, the Maple Leaf, *Quadrula*

quadrula, and the Monkey-face, *Quadrula metanevra*, were among the more resistant. However, the mortality rapidly approached 90 per cent or more for all species when the silt layer began to permanently cover the sand or gravel. On the other hand the mortality of the mussels in the crates was very low.

Laboratory experiments with fresh-water mussels in water carrying heavy loads of erosion silt (this material being kept in suspension by automatic glass stirring devices) showed that erosion silt interfered with the feeding of fresh-water mussels. The mussels in the muddy water remained closed a large per cent of the time, 75 to 95 per cent, while mussel in silt-free water but subject to the same current influences as those in the erosion silt tests were closed less than 50 per cent of the time. When mussels opened in water carrying large amounts of erosion silt, an excessive secretion of mucous was produced and this served in part to remove the silt which tended to settle into the mantle cavity. Mussels dying in silt laden water always contained deposits of silt in the mantle cavity and frequently in the gill chambers.

Retention of Organic Matter and Other Material by Erosion Silt

By a laking process organic particles and other substances in the river water are carried to the bottom as the silt settles out, and water-logged objects at the bottoms of streams are quickly covered by layers of silt, especially in the quieter waters. As a result organic matter, either from the natural detritus in the stream or from other sources, and trades wastes, as chemical and gas factory effluents, are carried to the bottom of the streams by erosion silt. Often these substances brought down with the silt are incompletely decomposed or are chemically unsaturated, so that subsequently large demands are made on the oxygen supply of the river water or noxious compounds are formed in these mud deposits. These hazards to aquatic life exist to some extent even in streams relatively free from erosion silt but are greatly augmented by the accumulation of material and the reduction of oxidation for which the silt blanket is responsible. The extent of the organic deposit held by erosion silt may be seen from some analyses of muds dredged from Lake Keokuk and Lake Pepin. These muds carried from 9.25 to 12.66 per cent organic material and from 0.286 to 0.457 per cent nitrogen by Kjeldahl determination in terms of dry weight. Erosion mud taken from surface run-off streams usually carried less than 1 per cent organic matter. Water analyses demonstrated low oxygen, high carbon dioxide and often relatively high sulphur content (as hydrogen sulphide or other sulphide derivatives) in water samples taken from near the bottom of these same river-lakes, above the layers of silt mixed with organic wastes, and bacteria counts made by the plate method showed that erosion silt deposits were much richer in bacteria than either the river water above these deposits, or the adjacent bottom areas of sand or gravel.

Laboratory experiments, verified these findings, for small amounts of

finely divided organic material when mixed with erosion silt created an oxygen demand in the surrounding water, which oxygen demand was maintained 10 to 15 times as long as the oxygen demand created by the same amount of organic material when mixed with fine sand. These experiments also demonstrated that disturbances in the pH and carbonate balances were also sustained over much longer periods when the organic material was carried down by erosion silt than when deposited with sand.

SUMMARY

1. Erosion silt alters aquatic environments, chiefly by screening out light, by changing heat radiation, by blanketing the stream bottom, and by retaining organic material and other substances which create unfavorable conditions at the bottom.

2. The present erosion silt loads of our inland streams have reduced the millionth intensity depth for light penetration from 15,000 mm. to 34,000 mm. or more, to 1,000 mm. or less, the summer average for the Mississippi River (1934) above Alton, Illinois being less than 500 mm.

3. Erosion silt in river water acts chiefly as an opaque screen to all wave lengths of visible light, but in very muddy waters a small differential was found favoring the transmission of scarlet-orange light.

4. Erosion silt alters the rate of temperature change in river waters. This is particularly significant in deep river lakes where thermal stratification of the water produces a stratification of the silt load, a warm muddy river, the hyperlimnorrheum flowing over a clear, cold lake, the hypolimnion, during the summer months.

5. Excepting the very quiet portions, erosion silt is quite uniformly distributed throughout the waters of rivers even in very deep holes, and in those river lakes in which there is no thermal stratification.

6. Erosion silt does not materially alter the salt complex or the amount of electrolytes in river waters.

7. Experimental studies demonstrated that layers of fine silt from one fourth of an inch to one inch thick produced a very high mortality among fresh-water mussels living in gravel or sand beds, and in water which was otherwise favorable.

8. The amount of organic material carried to bottom with erosion silt ranged from 8 to 12 per cent of the dry weight of the mud on the bottom of Lake Pepin and Lake Keokuk.

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A COMPARISON OF TWO VIRGIN FORESTS IN NORTHWESTERN PENNSYLVANIA

H. F. MOREY

*Allegheny Forest Experiment Station, United States Forest Service*¹

Pitifully little remains of the once extensive forests of white pine, *Pinus strobus* L., and hemlock, *Tsuga canadensis* (L.) Carr., that once made northern Pennsylvania famous as a lumbering region. Virgin stands that contain pine are extremely rare. Two of the most extensive, of incalculable value, are now in public ownership. Because both have been referred to as illustrations of the original forests of the Allegheny Plateau, a comparison of their composition and development is of interest.

Hearts Content, an area of 121 acres, is located in southern Warren County, and is part of the Allegheny National Forest. Cook State Forest Park,² a 6,000-acre tract of which 150 acres approach a virgin condition (Illick, '30), is situated in northeastern Clarion County and southwestern Forest County,³ some 20 miles south of Hearts Content. It is owned and administered by the state of Pennsylvania (fig. 1).

GEOLOGY, CLIMATE, AND PHYSIOGRAPHY

Hearts Content and Cook Forest are of similar geological origin, being a portion of the Pottsville uplift that formed the Allegheny Plateau. The soils, ranging from sandy loams to clay loams in the DeKalb series (Wilder *et al.*, '08, '11), were formed by the slow disintegration and decomposition of the Pocono sandstone and Pottsville conglomerate. Although outcropping of bed rock is common to both areas, it is more frequent at Cook Forest.

The climate in both localities is very much the same (Morey, '31a). Average annual precipitation is about 44 inches at Hearts Content and perhaps 2 inches less at Cook Forest. At both places the average summer temperature is 66° F.; the average summer precipitation is between 16 and 17 inches; and the average growing season is 135 to 150 days.

Hearts Content, at an elevation of 1,800 feet, lies at the very head of Tionesta Creek, a tributary of the Allegheny River. Cook Forest, 400 feet

¹ Maintained at Philadelphia, Pennsylvania, by the United States Department of Agriculture in cooperation with the University of Pennsylvania.

² Acknowledgment is due to Assistant Silviculturist O. M. Wood of the Allegheny Forest Experiment Station for the use of unpublished data concerning Cook Forest, obtained during 1930 in a tally and description of 14 strip plots of ½-acre each.

³ The portion of Cook Forest studied lies in northeastern Clarion County near the Forest County line.

lower in elevation, lies on Thoms Creek, close to its junction with the Clarion River. The Clarion is another tributary of the Allegheny, which it joins 40 miles below the mouth of Tionesta.

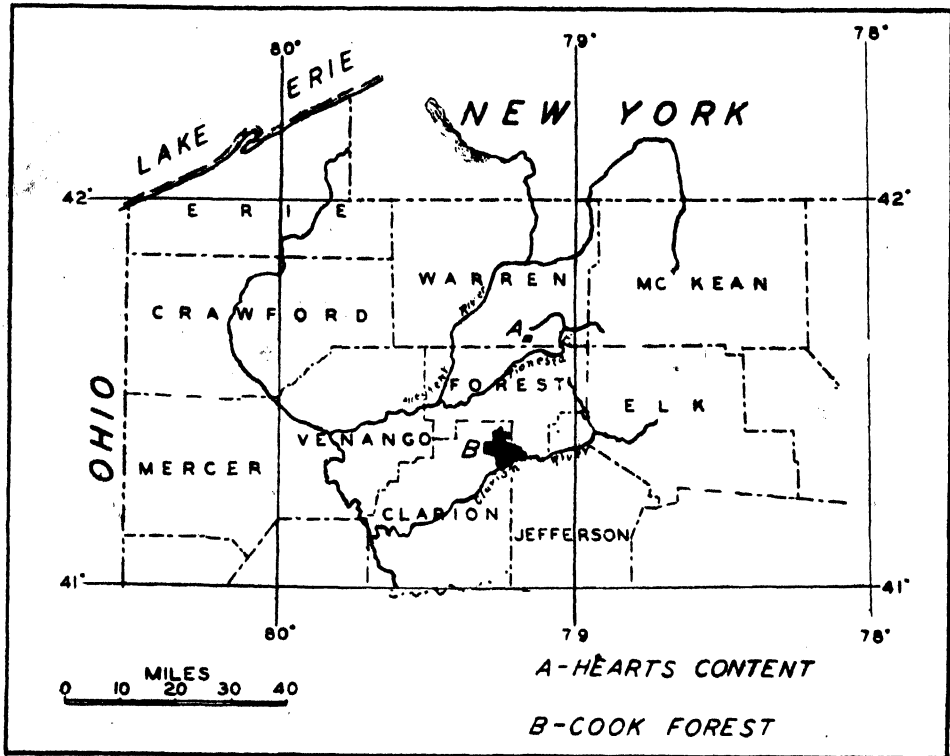


FIG. 1. Map showing the location of Hearts Content and Cook Forest in Pennsylvania.

The slope at Cook Forest varies from 5 to 50 per cent. The exposure varies considerably throughout the whole area, but is westerly in the portion of the stand studied by Wood. The slope at Hearts Content varies from 2 to 5 per cent in the hemlock consociation⁴ to 5 to 15 per cent in the hemlock-beech association. The exposure varies from a cove bottom in the consociation, to southeast, northeast, and northwest in the association.

HUMAN INFLUENCE

Both Hearts Content and Cook Forest show the evidence of human invasion in the form of scattered stumps. Dead trees have been removed from both areas, the average basal area per acre being about 40 square feet in each case. Felling of large trees and skidding of the logs cannot but have caused some disturbance of the litter, humus, and soil.

⁴ Hearts Contents was divided into two areas by Lutz ('30a), the hemlock consociation (70 per cent or more of the trees 10 inches and above in diameter being hemlock) on low ground, and the hemlock-beech association on higher ground.

Fires are known to have occurred in portions of both areas. Very old scars (charred) were discovered by Wood on some of the largest white pine at Cook Forest, although no evidence of recent fires has been found there. Jennings ('28) advances the theory that the oldest white pines at Cook Forest may have been established on a burn. At Hearts Content the last fire of any extent occurred in 1872 in the hemlock-beech association. No evidence of fire at any time has been found in the hemlock consociation.

PRESENT COMPOSITION

Environment and past history of the two stands are in general uniform enough to warrant the expectation of uniformity in the composition of the vegetation, or at least only such variations as are easily accounted for either by minor differences in these factors, or difference in the stage of succession. Major dissimilarities would certainly point to inadequacy of the samples; in other words, the tracts would appear too small to be really representative of the virgin pine and hemlock forests of northwestern Pennsylvania.

A comparison of the species appearing in both areas has been made.⁵ Unfortunately a statistical comparison of more than the arborescent species cannot be made, for neither frequency nor abundance of the various species of lesser vegetation is available for Cook Forest.

Before this comparison is made a point of controversy in the use of terms will be discussed. Both areas lie in the Transition or Allegheny life zone of Merriam (1898), which is the meeting ground for certain species of northern and southern flora. No argument would arise if the range of each species were confined to a single life zone, but since this is not true, controversial issues concerning the geographical nomenclature as applied to a species do occur. For example, the terms "southern" and "northern" as applied to beech, *Fagus grandifolia* Ehrh., are extremely controversial. Thus Sargent (1880) refers to beech as a southern species and Jennings ('27) speaks of the "more southern broadleaved type of forest (in southwestern Pennsylvania), characterized in various stages of its development by oaks, hickories, beech, etc.," whereas Merriam (1898) states, "In the Alleghenian faunal area the chestnut, walnut, oaks, and hickories of the south meet and overlap the beech, birch, hemlock, and sugar maple of the north." Such con-

⁵ This comparison is based on lists given for Hearts Content by Lutz (1930a, b; 1934), and for Cook Forest by Jennings (1928). Additional species found at Hearts Content by the author are: black gum, *Nyssa sylvatica* Marsh., chestnut oak, *Quercus montana* Willd. (listed by Jennings as "*Quercus prinus*"), and sassafras, *Sassafras variifolium* (Salisb.) Ktze. Additional species found at Cook Forest not recorded by Jennings but recorded by O. M. Wood, 1930, are: partridge berry, *Mitchella repens* L., smartweed, *Polygonum hydropiper* L., Christmas fern, *Polystichum acrostichoides* (Michx.) Schott, black cherry, *Prunus serotina* Ehrh., Virginia creeper, *Pseuderacemata quinquefolia* (L.) Greene, red oak, *Quercus borealis maxima* (Marsh.) Ashe, blackberry, *Rubus allegheniensis* Porter, common elder, *Sambucus canadensis* L., and wake-robin, *Trillium erectum* L.

fusion might be avoided if a species were a dominant member of a community in but one life zone, but again this is not true, for beech may be a prominent member of the Carolinian as well as of the Alleghenian life zones (Society of American Foresters, '32). Brown ('21) and Bray ('30) list beech as an indicator species of the "Alleghenian-Transition forest zone" as distinguished from the "zone of dominance of oaks, hickories, chestnut, tulip tree, etc." To a less extent the same controversy has arisen concerning the life zone of other species such as basswood *Tilia glabra* Vent., black cherry, *Prunus serotina* Ehrh., and white ash, *Fraxinus americana* L.

A given species should be assigned to that life zone in which it grows in greatest abundance. No data of the relative abundance of the several species are available, but relative abundance should closely follow lumber production. Assuming that such a relationship occurs, the lumber production data for 1925 (U. S. Forest Service, '27) were used in assigning the questionable species to a given life zone.

There are 93 herbaceous, shrub, and tree species that are common to both Hearts Content and Cook Forest. The Carolinian or more southern tree species are represented by the white oak, *Quercus alba* L., red oak, *Q. borealis maxima* (Marsh.) Ashe, chestnut oak, chestnut, *Castanea dentata* (Marsh.) Bork., black gum, sassafras, and cucumber magnolia, *Magnolia accuminata* L. The Alleghenian or more northern trees are represented by the beech, sweet birch, *Betula lenta* L., yellow birch, *B. lutea* Michx., red maple, *Acer rubrum* L., sugar maple, *A. saccharum* Marsh., service berry, *Amelanchier canadensis* (L.) Medic., pin cherry, *Prunus pennsylvanica* L.f., and black cherry.

The Carolinian white ash and yellow poplar, *Liriodendron tulipifera* L., are among the ninety-one species that are recorded for Hearts Content which have not been reported for Cook Forest.

Fifty-seven species have been found at Cook Forest which have not been recorded for Hearts Content. These include the Alleghenian species: striped maple, *Acer pennsylvanicum* L., mountain maple, *A. spicatum* L., speckled alder, *Alnus incana* (L.) Muench., basswood, pitch pine, *Pinus rigida* Mill., bear oak, *Quercus ilicifolia* Wang., and white grained mountain rice, *Oryzopsis asperifolia* Michx., and the Carolinian species: butternut, *Juglans cinerea* L., and scarlet oak, *Quercus coccinea* Muench. According to Jennings ('28) the mountain rice has been found at but two other places in Pennsylvania,—Presque Isle on Lake Erie and Bear Meadows in the central part of the state.

Unfortunately no exact comparison of the abundance of the smaller reproduction below one inch d.b.h.⁶ can be made between Cook Forest and Hearts Content, because Wood and Lutz used entirely different methods of collecting their data. Table I, which lists the number of milacres upon which a given species was dominant at Cook Forest, shows that the Alleghenian species dominate the young growth. This is similar to the conditions at Hearts Content (Lutz, '30a).

⁶ The abbreviation "d.b.h." refers to "diameter breast high."

TABLE I. *Dominant reproduction under a virgin forest stand, Cook Forest*¹

Species	Number of milacres upon which dominant	Percentage
Hemlock.....	313	44.7
Red maple.....	125	17.9
Sweet birch.....	75	10.7
Beech.....	59	8.4
Chestnut.....	15	2.1
Black cherry.....	12	1.7
Red oak.....	6	0.9
Yellow birch.....	4	0.6
White oak.....	2	0.3
White pine.....	1	0.1
No reproduction.....	88	12.6
Totals.....	700	100.0

¹ From O. M. Wood, 1931. Manuscript on 1930 examination of Cook Forest.

Sweet birch, red maple, beech, and black cherry reproduction is more abundant in Cook Forest than in either of the Hearts Content communities. The oak reproduction at Cook Forest, though sparse, is more abundant than that at Hearts Content. In fact, white oak reproduction is entirely lacking in the latter area.

DENSITY OF STAND

Table II shows that Cook Forest contains more trees per acre than either community at Hearts Content. Not only is this true for the smallest diameter class, but it is also true for the largest. However, both communities at Hearts Content have more trees in the 4-9 inch diameter class than Cook Forest.

From unpublished studies of diameter and age of the trees in the cut-over area adjacent to Hearts Content, it is evident that many of the beech, red maple, sweet birch, cucumber magnolia, and some of the hemlock comprising the 4-9-inch d.b.h. class in the beech-hemlock association there were established after the 1872 fire. However these same species in this class in the hemlock consociation were established sometime previous to 1872. Why the hemlock consociation should have a higher proportion of trees in this class than Cook Forest is not known.

It is noted (table II) that the species comprising the 4-9-inch d.b.h. class at Cook Forest consist almost entirely of the shade tolerant hemlock and beech. It is not improbable that at the time of the establishment of the individuals in this class, the shade was so dense and the root competition was so severe as to exclude the reproduction of the other species. As the stand became more open, due to the death of the dominant trees, the reproduction of the less tolerant species, such as the black cherry, probably became established, and now appears in the 1-3-inch class.

There are almost as many hemlock 10 inches and above in Cook Forest as in the hemlock consociation at Hearts Content. Cook Forest, however, has more hemlock in the smaller diameter classes than has either community at Hearts Content.

TABLE II. Average number of living trees per acre in Hearts Content and Cook Forest

Species	Hearts Content				Cook Forest							
	Beech-hemlock association				Hemlock consociation							
	Diameter breast high class, inches											
	1-3'' ¹	4-9'' ²	10''+ ²	Total	1-3'' ³	4-9'' ⁴	10''+ ⁴	Total	1-3'' ⁵	4-9'' ⁶	10''+ ⁶	Total
Hemlock	84.12	8.16	22.16	114.44	13.51	21.42	58.30	93.23	172.86	24.43	51.43	248.72
Beech	250.00	30.08	14.56	294.64	94.59	12.88	2.54	110.01	75.71	5.57	2.28	83.56
White pine			6.88	6.88			3.96	3.96	4.29		45.02	49.31
Red maple	27.78	5.60	6.72	40.10	32.43	2.00	.84	35.27	104.29	.85	.71	105.85
Sugar maple	3.17	.40	.16	3.73								
Sweet birch	19.84	6.24	1.60	27.68	37.83	7.98	1.68	47.49	122.86			122.86
Yellow birch	3.17	1.04	.08	4.29	70.27	14.00	2.84	87.11	1.43		.43	1.86
White oak			1.12	1.12					2.86			2.86
Red oak79	.40	1.12	2.31								
Cucumber magnolia	6.35	1.76	1.28	9.39	10.81	2.56		13.37				
Chestnut	1.59	5.52	5.52	12.63					1.43	.14		1.57
Black cherry	7.94	.56	.64	9.14	2.70	2.56	.56	5.26	15.71			15.71
White ash	3.17	.16		3.33		.28		.84				
Witch hazel	18.25	.08		18.33	24.32	.28		24.32				
Service berry79			.79	2.70			2.70				
Mountain holly												
Total number	426.96	60.00	61.84	548.80	289.16	63.96	70.72	423.84	501.44	30.99	99.87	632.30

¹ Based on 126 1/100th-acre plots.

² Based on 25 1/2-acre plots.

³ Based on 37 1/10th-acre plots.

⁴ Based on 7 1/2-acre plots.

⁵ Based on 14 5/100th-acre plots.

⁶ Based on 14 1/2-acre plots.

TABLE III. *Percentage of living trees per acre by diameter classes, Hearts Content and Cook Forest*

Species	Hearts Content					Cook Forest						
	Beech-hemlock association					Hemlock consociation						
	Diameter breast high class, inches											
	1-3"	4-9"	10"+	Total	1-3"	4-9"	10"+	Total	1-3"	4-9"	10"+	Total
Hemlock	19.71	13.60	35.83	20.86	4.67	33.49	82.44	22.00	34.48	78.84	51.50	39.34
Beech	58.56	50.14	23.54	53.70	32.72	20.14	3.59	25.96	15.10	17.97	2.28	13.22
White pine			11.12	1.25			5.60	.93	.86		45.08	7.80
Red maple	6.51	9.33	10.87	7.31	11.22	3.12	1.19	8.32	20.80	2.74	.71	16.74
Sugar maple	.74	.67	.26	.68								
Sweet birch	4.65	10.40	2.59	5.04	13.08	12.48	2.38	11.20	24.50			19.43
Yellow birch	.74	1.73	.13	.78	24.30	21.89	4.03	20.55	.28		.43	.29
White oak			1.81	.20					.57			.45
Red oak	.18	.67	1.81	.42								
Cucumber magnolia	1.49	2.93	2.08	1.71	3.74	4.00		3.15				
Chestnut	.37	9.20	8.93	2.30	.93	4.00	.79	1.24	.28	.45		.25
Black cherry	1.86	.93	1.03	1.66		.44		.20	3.13			2.48
White ash	.74	.27		.61				5.74				
Witch hazel	4.27	.13		3.34	8.41	.44		.07				
Service berry	.18			.14	.93			.64				
Mountain holly												
Percent of total	100	100	100	100	100	100	100	100	100	100	100	100
Total number of trees	426.96	60.00	61.84	548.80	289.16	63.96	70.72	423.84	501.44	30.99	99.87	632.30

White pine in the larger diameter classes is much less abundant at Hearts Content than at Cook Forest. In fact, white pine and hemlock constitute over 96 per cent of the Cook Forest stand of 10 inches and above in diameter (table III).

Although sugar maple and yellow birch are found in Cook Forest, they are rare in the main stand. No individuals of these species in the one-inch d.b.h. class or larger were found on any of the sample plots in Cook Forest. Sugar maple is also absent from the hemlock consociation at Hearts Content.

BASAL AREA PER ACRE

Cook Forest has a greater basal area per acre in both living and dead trees than either community at Hearts Content (tables IV and V). Lutz concludes ('28) that the significance of basal area would indicate that Cook Forest is more advanced successionally than Hearts Content. The writer does not believe this to be true, for the fact that nearly 62 per cent of the basal area (living trees 4 inches and above d.b.h.) at Cook Forest is white pine, a species reproducing to an extremely small extent, does not suggest approach to a stable composition. The highest proportion of basal area of white pine found at Hearts Content is 26 per cent in the beech-hemlock association. White pine is reproducing very poorly at Hearts Content also.

TABLE IV. *Average basal area per acre, living trees 4 inches D.B.H. and above, Hearts Content and Cook Forest*

Species	Hearts Content				Cook Forest ³	
	Beech-hemlock association ¹		Hemlock consociation ²			
	Sq. ft.	Per cent	Sq. ft.	Per cent	Sq. ft.	Per cent
Hemlock.....	64.57	39.68	138.51	75.33	100.20	36.00
Beech.....	24.63	15.13	5.10	2.77	3.43	1.23
White pine.....	41.68	25.62	27.93	15.18	172.16	61.85
Red maple.....	13.71	8.42	1.83	1.00	1.08	.39
Sugar maple.....	.24	.15				
Sweet birch.....	2.30	1.41	2.90	1.58	0.83	0.30
Yellow birch.....	.29	.18	6.01	3.27		
White oak.....	3.26	2.00			.65	.23
Red oak.....	2.78	1.71				
Cucumber magnolia..	1.55	.95	.38	.21		
Chestnut.....	6.89	4.23			No trees above 2"	
Black cherry.....	.82	.50	.42	.23		
White ash.....	.02	.01	.75	.41		
Serviceberry.....			.04	.02		
Witch hazel.....	.01	.01				
Total.....	162.75	100.00	183.87	100.00	278.35	100.00

¹ Based on 25½-acre plots.

² Based on 7½-acre plots.

³ Based on 14½-acre plots.

TABLE V. *Average basal area per acre, stumps and dead trees 4 inches D.B.H. and above, Hearts Content and Cook Forest*

Species	Hearts Content ¹				Cook Forest ²	
	Beech-hemlock association		Hemlock consociation			
	Sq. ft.	Per cent	Sq. ft.	Per cent	Sq. ft.	Per cent
Hemlock.....	1.71	10.39	.79	20.63	25.68	43.31
Beech.....	.25	1.52			.23	.38
White pine.....	3.37	20.49	3.00	78.33	33.19	55.98
Red maple.....	.17	1.03			.20	.33
Sweet birch.....	.04	.24				
White oak.....	1.32	8.02				
Cucumber magnolia..	.10	.61				
Chestnut.....	9.49	57.70	.04	1.04		
Total.....	16.45	100.00	3.83	100.00	59.30	100.00

¹ Taken from Lutz (1930a) table VII.² Based on 14½-acre plots.

Hemlock constitutes from 40 to 75 per cent of the basal area (respectively in the beech-hemlock association and the hemlock consociation) at Hearts Content, but includes only 36 per cent of the basal area at Cook Forest. In this respect, Cook Forest is similar to the beech-hemlock association.

Although the basal area of the beech and red maple at Cook Forest is similar to that in the hemlock consociation, it is much less than that in the beech-hemlock association at Hearts Content. This is also true for most of the remaining species, all hardwoods.

The proportion of basal area of the dead hemlock (table V) is much greater at Cook Forest than at Hearts Content. The author believes that this death is natural, being due to overmaturity. Groups of large, overmature hemlock, dying or dead, have been observed by the writer in a virgin stand of hemlock-hardwoods in southeastern Warren and southwestern McKean counties in northwestern Pennsylvania (Hough, '36).

Although the basal area of dead white pine is greater at Cook Forest than at Hearts Content, the proportional basal area is much higher in the hemlock consociation than in either of the other communities. The death of the overmature white pine in these areas, with little or no establishment of white pine reproduction is evidence that white pine is making its last stand at both Hearts Content and Cook Forest.

The proportional basal area of living and dead chestnut is much greater in the beech-hemlock association than at Cook Forest. In fact there was no chestnut above two inches d.b.h. in the Cook Forest Plots. Most of the chestnuts at Hearts Content are sprouts, many of which no doubt followed the killing of the parent trees by fire (fig. 2). There have been no comparatively recent fires at Cook Forest to cause sprouting of chestnut.

AGE OF THE PINE

Twenty-three stumps of cut dead white pine, examined at Cook Forest, averaged 232 years of age or about the same as the average age of the white pine at Hearts Content. Several large white pine at Cook Forest have been estimated independently by Jennings and the station to be about 400 years old.

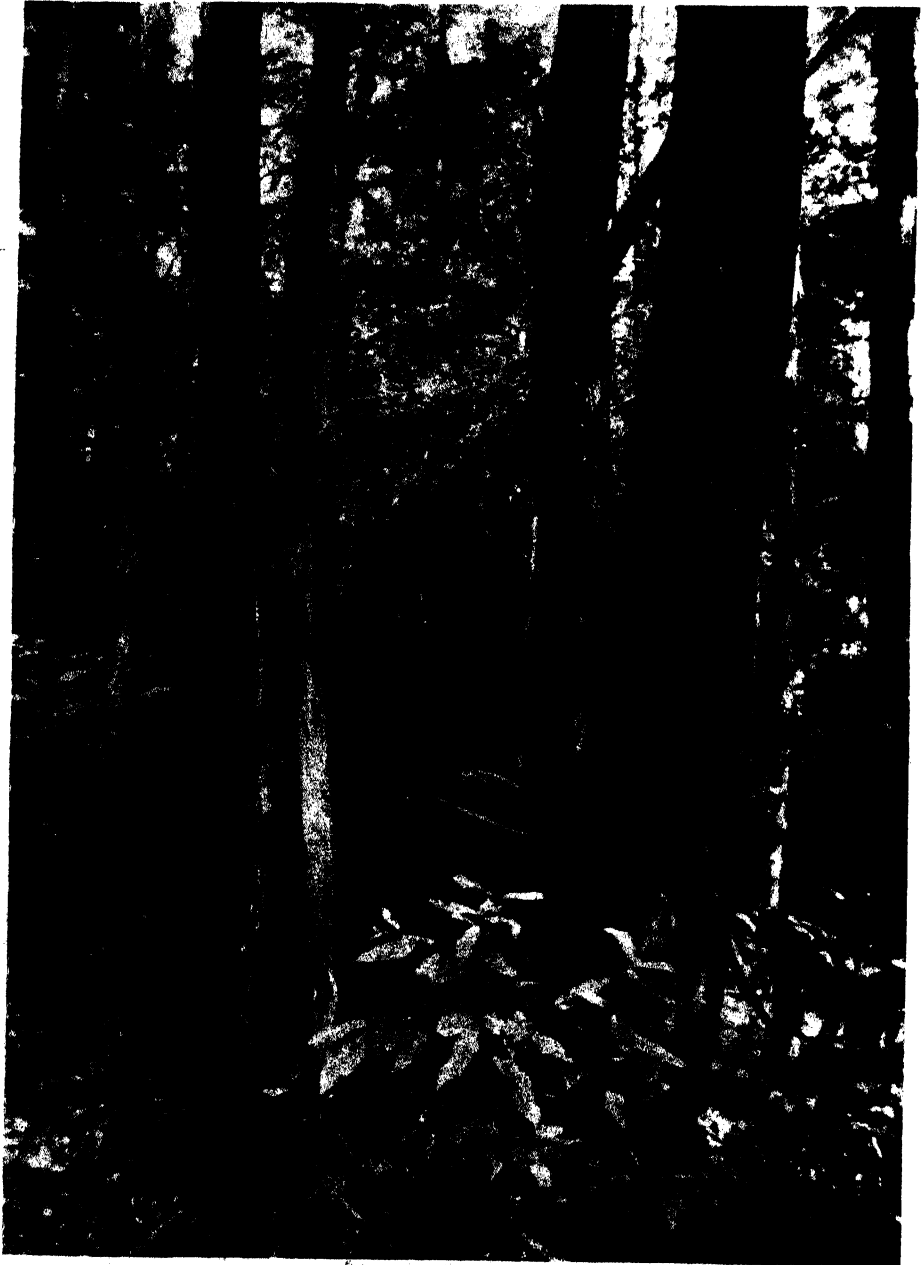


FIG. 2. Chestnut sprouts in the beech-hemlock association which followed the fire of 1872. Note the remnants of the fire-killed parent tree in the center of the clump.

The oldest pine found at Hearts Content was 292 years of age, a century younger.

The pine at Cook Forest appears to be even-aged, and that at Hearts Content apparently comprises even-aged groups (Morey, '31b).

PROBABLE SUCCESSION OF CLIMAX COMMUNITIES

Three associations of two formations are represented in the ecotone (tension zone) of which Cook Forest and Hearts Content are a part. These are the *Pinus-Tsuga* association (pine-hemlock forest) of the *Pinus-Tsuga* formation (Lake forest), and the *Acer-Fagus* (maple-beech forest) and *Quercus-Castanea* (oak-chestnut forest) associations of the *Quercus-Fagus* formation (deciduous forest). Such a complexity of composition makes the determination of present successional trends difficult, but a brief review of the effects of glacial movement upon the migration of vegetation tends to clarify the situation.

It is generally recognized among geologists and ecologists that vegetation recedes from the advance of a glacier and advances into the area previously occupied by the glacier when it recedes. Consequently there is a theory that the northward migration of vegetation following a glacial period comprises various waves of vegetation each of which would be composed of vegetation of a distinct life zone (Adams, '02 and Harshberger, '11). If this theory is tenable it is possible that as the climate becomes more or less stabilized the rate of vegetative migration becomes much retarded and may finally cease.

The following theory is advanced concerning the probable succession at Hearts Content and Cook Forest. The *Pinus-Tsuga* association occupied that portion of the Allegheny Plateau previous to its invasion by members of the *Acer-Fagus* association whose northward migration may have been either along the stream valleys, along the higher elevations, or both. As the climate became warmer with the further recession of the glacier to the north, members of the *Quercus-Castanea* association invaded the region by migrating up the warmer valleys which they now occupy. This invasion continued, even to elevations as high as 1,800 feet as at Hearts Content, until the region became a great transition zone. The *Pinus-Tsuga* association in this zone became decadent to such an extent that only relict areas containing it, such as the hemlock consociation, may now be found. Lutz ('30a) suggests that the hemlock consociation at Hearts Content may be a *physiographic climax*. At the higher elevations *Quercus-Castanea* association will gradually give way to the *Acer-Fagus* association which will dominate the zone until some future disturbance occurs.

Jennings ('27, '28) suggests that the red and white oaks are still extending their range by slowly migrating northward. This may be true in the river valleys, but does not appear to be true at Hearts Content or Cook Forest. Evidence that pine, oak, and chestnut reproduction is sparse or absent while

⁷ The passing of the chestnut has of course been hastened by the chestnut-blight.

hemlock, beech, red maple, and birch reproduction is abundant, and that white pine is dying in both areas indicates that the migration of the *Quercus-Castanea* association has apparently passed its climax and is now becoming decadent with the *Pinus-Tsuga* association (hemlock as a species being excepted), while the *Acer-Fagus* association is slowly establishing itself there.

Although the hemlock is a frequent associate of both the maple and the beech, it is regarded by Weaver and Clements ('29) as being a relict of a former southward extension of the *Pinus-Tsuga* formation. It appears that at Cook Forest and Hearts Content a balance is maintained between the hemlock and the beech-maple. (The red maple instead of the sugar maple is the associate of the beech in these two localities, yet sugar maple appears to be increasing in abundance at Hearts Content.)

From the evidence at hand the writer believes that a hemlock consociation and a beech consociation or beech-maple association are climax communities in the ecotone between the Lake forest and the Deciduous forest formation, which are converted cyclically from one to the other. There is evidence that the hemlock at Hearts Content comprises even-aged groups (Morey, '31b) and the author has observed a pronounced grouping of hemlock at Wetmore, Pennsylvania.⁸ The hemlock, being very tolerant, is able to persist for many years under the shade of the hardwoods (beech, birches, maples). When these hardwoods are removed, either by wind or by natural death, the understory of hemlock becomes a portion of the crown canopy, which casts so much shade and may offer so much root competition as to prevent the establishment of even hemlock reproduction. When the hemlock groups become overmature, they gradually die, or sometimes are windthrown, allowing the hardwoods to become established. This cycle probably continues until some major catastrophe, such as a general windfall, fire, cutting, insect, or fungous epidemic occurs, when retrogressive succession begins.

SUMMARY

A comparison was made between Cook Forest and Hearts Content, two virgin forests lying in the Alleghenian life zone in northwestern Pennsylvania.

Ninety-three species have been recorded as common to both communities, ninety-one species recorded for Hearts Content but not for Cook Forest, and fifty-seven species recorded for Cook Forest but not for Hearts Content.

Hearts Content has a much lower percentage of white pine, a smaller number of trees per acre, and a smaller basal area per acre than has Cook Forest.

Although key species of the *Pinus-Tsuga* and *Quercus-Castanea* associations are found at Hearts Content and Cook Forest, there is evidence that the establishment of the white pine, oaks, and chestnut is now checked and that these species are being replaced by hemlock and members of the *Acer-Fagus* association in both areas.

⁸ It is not known at this time whether these groups are even-aged or all-aged.

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THE TOLERATION OF SOLAR HEAT IN DESERT REPTILES

WALTER MOSAUER

University of California at Los Angeles

Desert lizards have a remarkable reputation as animals seemingly immune to the terrific heat of the desert sun. Buxton ('23, p. 98), states that animals "manage to exist on the desert soil even in the middle of the day in summer. Good examples among the reptiles are the Agama lizard . . . and the Chuckwalla (*Sauromalus*), . . . which sits upon rocks when they are too hot for the hands to touch (Camp, '16)." Thomas ('32, p. 148) tells of a lizard which "delights to sit on the most glaring eminences in the face of the tropical sun towards which it nods its head. . . . This creature alone of all the steppe life that I met, scorns refuge from the sun." Werner ('13, p. 189) reports that *Acanthodactylus scutellatus* of the Sahara Desert shuns not even the noon heat in summer; he found it abroad in southern Morocco as the only animal besides a grasshopper, in the furnace heat of the afternoon in midsummer. Mosauer and Lazier ('33), reporting on death from insolation in desert snakes, stated: "It is interesting to note the extreme sensitivity to sunlight of these nocturnal desert reptiles which so sharply contrasts with the tolerance of certain diurnal reptiles, such as *Uma notata*, which, in exactly the same habitat, plays and thrives on sand at 55°-60° C."

All these statements would lead one to believe that lizards actually possess a greater tolerance to the desert sunshine, and the heat produced by it, than most other animals. But how could that be? Snakes are killed by a short exposure to the desert heat (Mosauer and Lazier, '33) and the lacertilians, belonging to the same order *Squamata*, could not be expected to have a fundamentally different mechanism for heat regulation. As poikilothermous animals, they cannot prevent their body temperature from assuming the same value, within a few degrees, as that of their environment. The mid-day temperatures of the desert soil, be it sand or not, frequently exceed 60° during spring, and the air within an inch of the surface is heated by radiation from the hot ground to a temperature considerably above the air temperature as conventionally registered.

Since the field observations of the authors quoted above and of many others, and the conditions just outlined seemed incompatible, the author decided to put the problem to experimental test.

MICROCLIMATIC CONDITIONS OF THE DESERT

In connection with the present study, it is of significance to examine samples of the microclimatic conditions in the habitat of the animals con-

cerned. The data compiled in the following charts were obtained in the course of an investigation of the 24-hour temperature cycle of kangaroo rat burrows. The air temperature and the humidity were recorded with an Assmann Psychrometer within an inch of the ground, in order to obtain a true picture of "climate" as valid for a small terrestrial animal such as a rodent or reptile. The temperature of the sand surface was measured by sprinkling the bulb of a thermometer with sand and leaving the instrument in place, or by rapidly rolling the thermometer along the surface of the sand; the readings obtained by both methods checked closely.

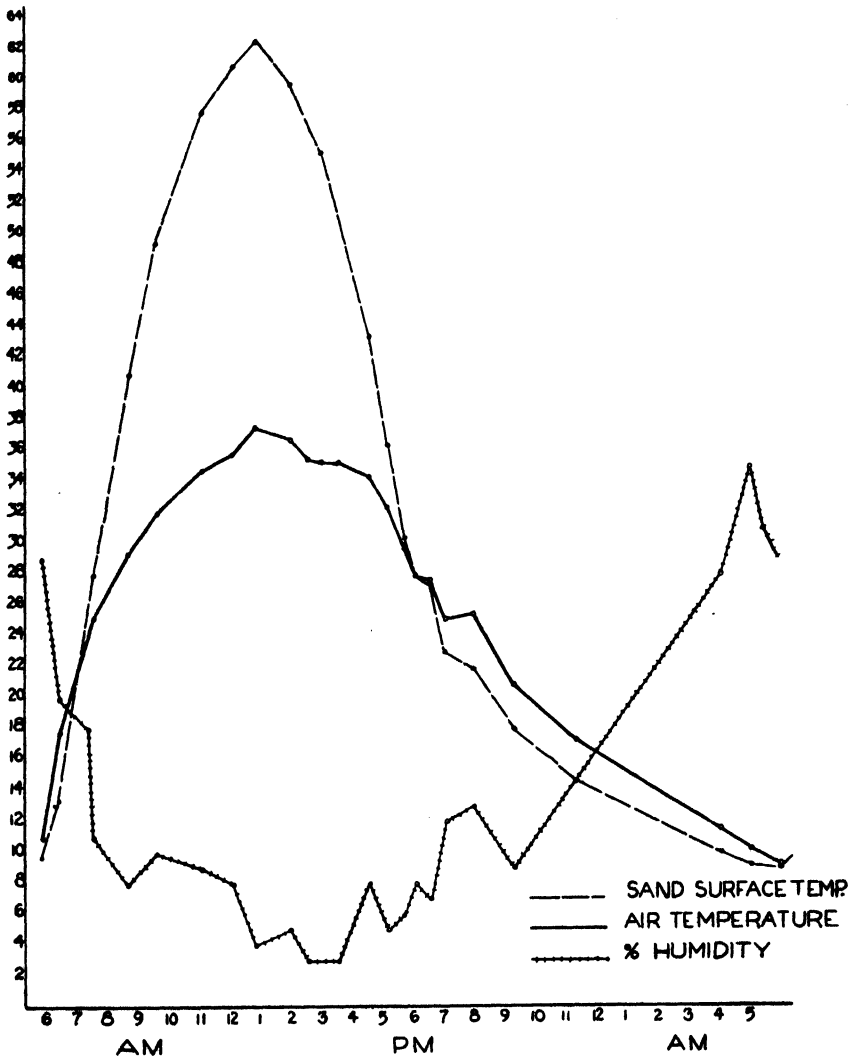


FIG. 1. Graph representing twenty-four hour recordings of air temperature close to the ground, sand surface temperature, and humidity, recorded on April 7-8, 1934, in the sand dunes near Indian Wells, Coachella Valley, California. The numerals on the ordinate represent centigrades in the case of the temperatures, percentages in the case of the humidity.

Figure 1 shows that even as early in the season as in the first part of April the sand surface temperature reaches and exceeds 60° C. during the noon hours; it also shows the tremendous difference between surface temperatures and the temperature of the air, even of that stratum very close to the ground.

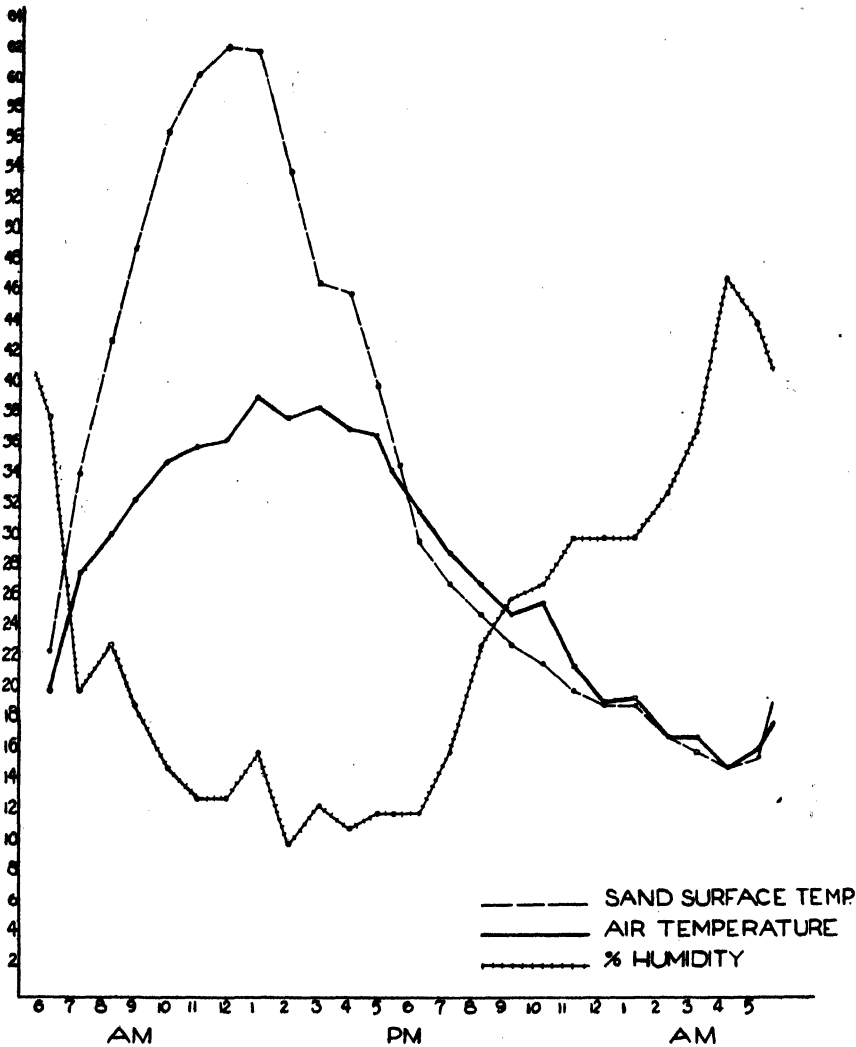


FIG. 2. Twenty-four hour cycle of air temperature, sand surface temperature, and humidity, recorded on April 19-20, 1934, in the Algodones dunes in Imperial Valley, west of Yuma, Arizona.

In figures 2 and 3, representing conditions somewhat later in the season, the curve of the surface temperature is not as steep and sharply peaked, indicating that the sand is heated beyond 60° for a longer period. The tremendous difference in humidity between day and night is also obvious from the charts.

LARORATORY EXPERIMENTS ON THE VITAL TEMPERATURE LIMITS OF
DESERT REPTILES

It would be conceivable that desert lizards have constitutionally a greater tolerance for high body temperatures than that found in other animals, since

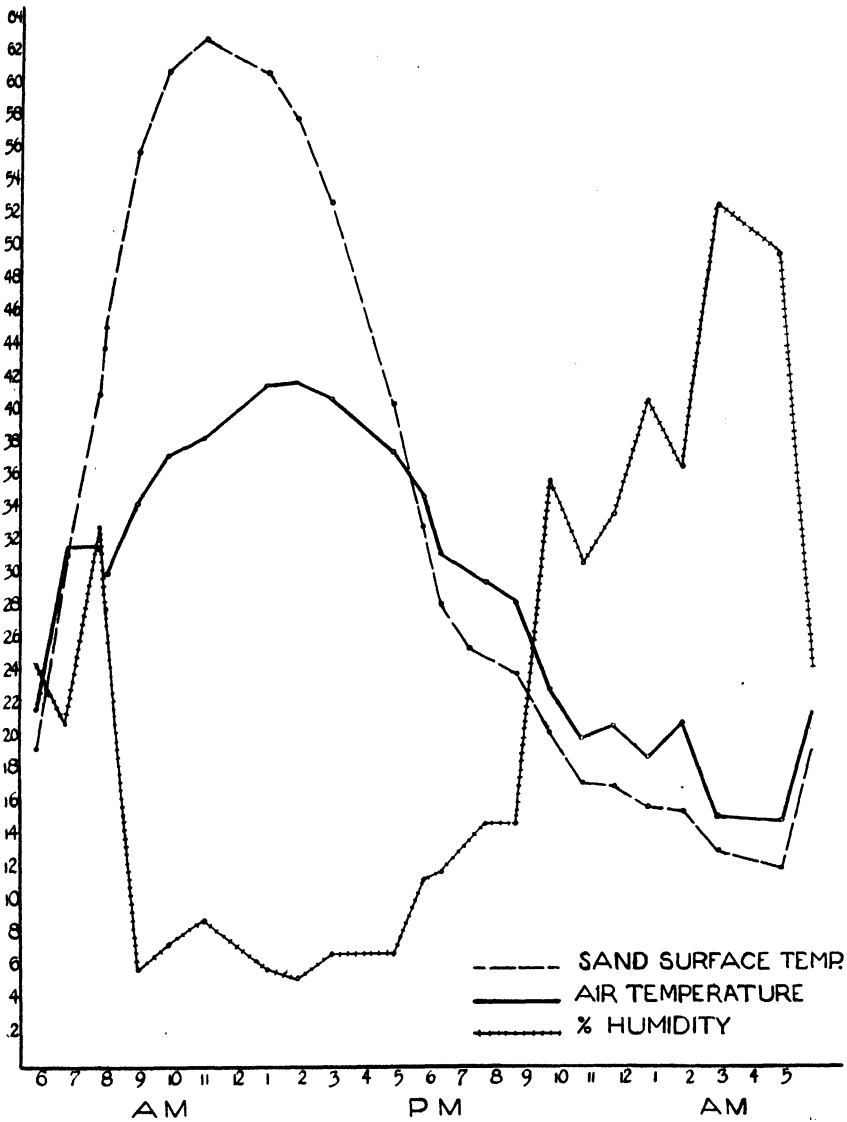


FIG. 3. Twenty-four hour cycle recorded on May 5-6, 1934, in the dunes near Indian Wells, California.

it is a well known fact that certain animals have become adjusted to the extreme temperatures of hot springs ; and that the normal body temperature of a bird corresponds to what would be a dangerous fever temperature in man. To test this possibility of an adjustment to high temperature, several desert reptiles

were subjected to overheating by means of the following arrangement. Two electric heating filaments were removed from the experimental cage described below (fig. 4) and were hung approximately 10 inches above the cage con-

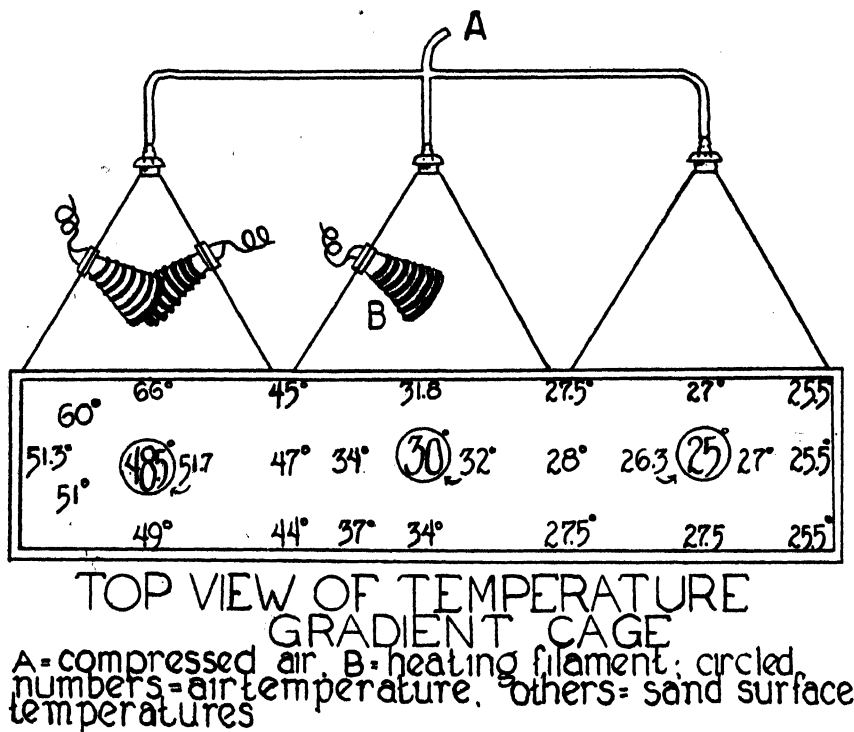


FIG. 4. Diagram of the cage used to determine the temperature preferences of desert reptiles experimentally.

taining the specimens. The latter represented two species of lizards, the Ocellated Sand Lizard (*Uma notata*, 5 specimens) and the Desert Iguana (*Dipsosaurus dorsalis*, 1 specimen) and one snake species, the Sidewinder (*Crotalus cerastes*, 4 specimens). The results showed no marked difference in heat toleration between the diurnal lizards and the nocturnal rattlesnake.

In an air temperature of 55° C. and a sand surface temperature of 60° lizards and snakes alike died within from 5.5 to 12.5 minutes, after the identical symptoms of gasping, polypnoea, extreme agitation, and finally convulsions.

The body temperature at the moment of death was in most cases measured by means of a thermocouple, the pointed end of which was pushed through the body wall into the body cavity; in some cases the rectal temperature almost immediately afterward was measured with a thermometer. The average of four thermocouple readings for *Uma* is a fraction over 45° (ranging from 44.2° to 45.7°), and almost identical with the average of four readings for the Sidewinder (with a range of from 44.8° to 45.7°). The

thermometer readings were somewhat higher, averaging 47° for three of the Sidewinders, and 51° for two *Uma*. This difference is undoubtedly due to the rapid rise in temperature just after death, and the lapse of a few seconds during the insertion of the thermometer bulb in the rectum. The thermometer readings for the Sidewinder check very well with the previous results (Mosauer and Lazier, '33).

Uma notata is a highly specialized sand reptile, and inhabits the barren, glaring dunes where the vegetative cover is reduced to the minimum, and shrubs of any size are restricted to the depressions between the dunes. The temperatures of the sand surface and the air close to the ground are very high during the day time when this lizard is active (figs. 1, 2, 3). The Sidewinder, on the other hand, is abroad after dark, at temperatures sometimes as low as 10° , and it seems surprising that there is no obvious difference in heat toleration between these two reptiles.

EXPERIMENTS IN THE NATIVE HABITAT

From the results given above it was obvious that the desert lizards have no inherent greater heat toleration than the nocturnal snakes. Still, it seemed possible that conditions in the actual habitat, not under artificial laboratory conditions, might give a different picture. In order to test this a freshly collected large specimen of *Uma notata* was fastened by soft string tied around its thighs, to a small stick, which was pushed into the sand on an open sunny sand-slope in the dunes near Kelso in the Mojave desert. This permitted the lizard some freedom of movement within a circle of 10 in. radius, and exposed it to the sunshine without altering in the least the typical microclimatic conditions, freely admitting any cooling air currents.

The date was the 4th of May, and the heat was considerably alleviated by a cool breeze which blew with short intermissions throughout the experiment. At 11.36 A.M. when the lizard was first placed on the sand, the air temperature registered 25° and remained the same, with fluctuations of not more than one degree. The sand surface varied in temperature from 45° to 49° , according to the change in wind intensity. The specimen remained at first perfectly quiet, lying flattened to the sand. At 11.48 it became alert, rose on its forelegs and slightly opened its mouth. Simultaneously, it turned up its hind toes and tail to avoid contact with the hot ground (Mosauer, '35, p. 19). A little later, the lizard quieted down and settled again flatter to the ground. At 12 M. it rose again, opened its mouth and attempted to run away for the first time. From then until 12.30 P.M., it remained alert with open mouth and frequent bursts of running. It made no attempts, however, to burrow in the sand. After 12.30, it directed all its running attempts towards the shade. At 12.34, it made a violent rush, turned over on its back and lay for approximately a minute in a distinct opisthotonic position, breathing rapidly and deeply. Then it righted itself, but repeated the procedure several

times. Apparently the excessive temperature was affecting its central nervous system (cerebellar centers of equilibrium and muscular coordination?). From 12.38 on, it seemed to have calmed down again, since no running attempts or convulsions were in evidence, but it was rather a condition of coma than of quiescence—shortly after 1.00 P.M. it was lying flat on the sand, with fore and hind legs stretched backward, eyes closed; respiration was infrequent and superficial. At 1.10 it was, from all appearances dead. Its body temperature, measured per anum, was 47°.

It took an hour and thirty minutes of continuous insolation to kill this lizard; it must be considered, however, that the sand temperature was mostly below or equal to, and only rarely exceeded, the body temperature which the laboratory experiments had shown to be critical for desert reptiles. Furthermore, the air temperature was quite moderate, and with the aid of the blowing breeze, with the cooling evaporation from its oral mucous membranes, and with the increased respiratory rate, the lizard managed to keep its body temperature below the critical point for a considerable time. Nevertheless, it registered discomfort 12 minutes after the beginning of the experiment, and would undoubtedly have made for the shade at that time, if free to move at will.

A more convincing case seemed desirable, however, and on June 2, 1935, opportunity was taken to repeat the experiment with a different desert lizard. In the sand dunes near Olancho, at the south end of Owen's Lake, a freshly collected adult male of *Callisaurus ventralis gabbii*, the Gridiron-Tailed Lizard, was fastened on the top of a dune in the manner described before. The air temperature registered 33° in the shade, and 38° one inch above the sunny sand; the surface of the sand registered 59°. The lizard was placed on the sand at 12.30 P.M., and attempted to run almost immediately; at 12.32.30 its mouth opened, and its movements became slightly discoordinated. At 12.33 it turned on its back and lay in opisthotonus, breathing violently; it remained in this position, with fore legs moving now and then, until the end of the experiment. At 12.39, its motions and respiration had stopped almost completely; the body temperature was measured and found to be 47.5°. The experiment was then interrupted and it was attempted to revive the specimen, which died, however, within half an hour.

If we correlate the outcome of these simple experiments with the tables of desert microclimate, we are forced to conclude that the field observations of desert reptiles have failed to bring out clearly the following points: (1) Lizards have no greater toleration of high air temperatures, substratum temperatures, and intensive insolation, than nocturnal snakes. (2) In their desert habitat, lizards could not spend more than a few minutes in the open, during the hotter time of the day, through spring, summer and fall, without suffering discomfort. (3) Consequently, observations of lizards active or "basking" during these periods, failed to take notice of the time actually spent by the lizards continually exposed to the sunshine.

FIELD OBSERVATIONS OF THE BEHAVIOR OF DESERT REPTILES

It is an unquestionable fact that one sees specimens of *Uma*, *Callisaurus*, *Dipsosaurus*, etc., on the open stretches of sand during the hotter hours of the day, but they are always rushing across the glaring sand towards the next shelter of shrub or burrow.

They are not usually seen before they begin running, and it seems reasonable to assume that all such specimens have been driven by our approach from some shelter, either from the shade of a shrub or from the deeper, cooler layers of sand in which they had lain buried. In a previous publication (Mosauer, '35a), I wrote concerning *Uma*, "... one does not see much of them during a ramble over the dunes at midday except for their tracks," but ascribed this fact to the apparent wariness and keen vision of this species.

Rapid locomotion is absolutely essential for these diurnal desert forms, because it enables them to travel from shrub to shrub across the intervening area of open sand quickly enough to avoid the dangers of overheating. Thus we find some of the lizards extremely fast runners, others at least fairly fast; the only truly diurnal desert snake is the Red Racer (*Coluber flagellum frenatum*), one of the fastest snakes of North America (Mosauer, '35a, p. 20, and 35b).

Generally speaking, the lizard has a decided advantage over the snake, because in locomotion only its feet and sometimes its tail touch the sand, while the main bulk of its body is elevated into a stratum of air much cooler than the burning surface of the sand. The snake, however, is in contact with the sand along most of its ventral surface, and consequently absorbs the heat of the ground more rapidly. This is not quite true of the Sidewinder (*Crotalus cerastes*) with its looping locomotion, in which only two sections of the body touch the ground (Mosauer, '30) yet the area of contact is relatively much greater than in a lizard. If a rattlesnake has coiled up and come to rest during the night on a certain spot, it will, of course, keep the sand beneath it from being heated after sunrise; if the snake has dug itself in so that its dorsal surface is level with the sand, and its peripheral coil is buried, then most of its body is in contact with cool sand, and only a small part of its integument is exposed to direct insolation. These points may explain the observation of Camp ('16) who found the Sidewinder "partly buried flush with the surface in the hot sand right out in the noonday sunshine of midsummer." It must be added, however, that the present author has been unable to verify Camp's findings, although he has collected nearly one hundred specimens of *C. cerastes*. On June 2, 1935, he collected three specimens in the sand dunes at Olancho, California, during the morning hours. The air temperature was 26.5°, the sand temperature was 25° in the shade, and rose in the sun from 37° to 42°. Although these temperatures are very low compared to those of noonday during midsummer (which must nearly double them) two of the three Sidewinders had abandoned their original resting places, easily recognizable by the

circular hollows in the sand, which were now in the full sunlight, and had coiled again, a foot away, in the shade of a bush. The third specimen was also resting in the shade, at the entrance of a rodent burrow.

SELECTION OF OPTIMUM TEMPERATURES IN AN EXPERIMENTAL CAGE

It was thought that the temperature preference shown by the lizards in an experimentally heated cage might be somewhat indicative in spite of the obviously artificial conditions, of the optimum temperature in the habitat. A cage was constructed which measured 92 cm. in length and 21 cm. in width, with the long side walls formed by screen wire. Along the whole length of one side were fastened three metal funnels of equal size, the wide openings of which occupied almost the entire area of this side wall, while the narrow openings were connected with the compressed air system.

The center funnel contained one electric heating filament, the left one contained two and the right funnel was without heating device. This arrangement made it possible to create a temperature gradient in the cage, blowing air through it which ranged from 25° at the right end to 60° at the left (fig. 4).

Several specimens of *Uma notata* were usually released simultaneously into this cage, and their positions were noted at certain intervals. Mostly they were found to aggregate in the middle third, towards the boundary of the left, hottest third of the cage. In the majority of cases, they buried themselves in the sand, sometimes leaving the head slightly exposed.

Counting each individual separately, 29 trials, besides the controls, were made. The places at which the lizards came to rest varied considerably in temperature, ranging from 26° to 43° for the sand and from 24° to 37° for the air. Most of the records for the sand temperature, however, ranged from 35° to 40°, averaging 37° for all trials, and the air temperatures were mostly between 28° and 37°, averaging 32°.

It must be understood, of course, that these temperatures are the ones, at which the lizards came to rest, and the optimum for activity is undoubtedly somewhat higher. In the field, specimens of *Uma* were found buried in sand of 37° to 43°, with body temperatures closely approximating the environmental temperatures. A correlation of the results of field observations, and experiments on optimum and lethal temperatures makes it likely that these latter are not very far apart. The optimum at which the lizard is most alert and active, ranges from 35° to over 40°, while a rise in body temperature over 45° is quickly fatal.

DISCUSSION

There can be little doubt that the lethal factor in insolation is simply thermic, and not the action of ultra violet rays, nor the effect of excessive desiccation due to evaporation of body fluids. The perfect agreement of the body temperatures at the time of death in the laboratory experiments, when the overheating is caused by an electric heater, and in the desert habitat, where

direct insolation and the heat of the ground are effective, seems evidence enough for this assumption. Buxton ('23) says, ". . . under natural conditions a high temperature and a low humidity are generally associated. . . . It is not therefore possible in the absence of experimental work, to discriminate between the effects of the two." Hall ('22) has shown, however, that desert reptiles can endure exsiccation to one-third of their original body weight, while the loss of fluid in the present experiments, lasting only a few minutes, is obviously negligible. The bodies of the animals show their full usual turgescence at an autopsy following thermic death. We might conclude from these facts, that it is the temperature, not the relative humidity and corresponding evaporation, which exerts the greater influence on animal life in the desert.

ACKNOWLEDGMENTS.

The work here presented was carried on as part of an investigation of the ecology of desert reptiles, and was supported by research grants of the University of California. Mr. Allan Cameron, my research assistant under the S. E. R. A. project, has helped me greatly in obtaining the data and tabulating the results. Dr. E. L. Lazier and Mrs. Mosauer have kindly assisted me in obtaining the 24-hour recordings of desert temperatures.

SUMMARY

1. Several species of desert reptiles, including the lizards *Uma notata*, *Dipsosaurus dorsalis*, and the snake *Crotalus cerastes*, were subjected to overheating by radiation from electric heat filaments. They were killed rapidly at environmental temperatures of 55° to 60° and their body temperature at death ranged from 44.2° to 53°. The average of thermocouple recordings for four *Uma* was the same as for four *Crotalus*, e.g. 45°.

2. A freshly collected specimen of the Ocellated Sand Lizard (*Uma notata*) was exposed to the sunshine in its native habitat. Although the day was unusually cool, with an air temperature of 25°, and a sand surface temperature of 45°-48°, it registered discomfort within 12 minutes, and was dead after 1 hour and 30 minutes. A specimen of the Gridiron-Tailed Lizard (*Callisaurus ventralis gabbii*) was killed by an exposure of 9 minutes, at an air temperature of 33° and a sand surface temperature of 59°. In both cases, the body temperature was approximately 47°.

3. Contrary to popular belief, the toleration of excessive temperatures by desert lizards is no greater than could be expected of poikilothermous reptiles, and no greater than that shown by nocturnal snakes.¹

4. The temperature of the sand surface in the Colorado Desert exceeds 50° between 9:00 A.M. and 3:30 P.M. even in early April, and rises above 60°

¹ After completion of this work, a paper by Dill, D. B., and co-authors ('35) came to my attention, in which they report findings very similar to those here presented, with the Chuckwalla (*Sauromalus obesus*) and the Horned Toad as subjects of their experiments.

for at least two or three hours around noon. These temperatures are highly uncomfortable, and dangerous after a short exposure, to the desert lizards examined. It is concluded that field observations reporting prolonged basking of lizards failed to record the length of time spent by the lizard exposed to the sunshine. The periods of greatest activity are undoubtedly the early morning and the afternoon.

5. In a temperature gradient cage, ranging from 25° to 60°, specimens of *Uma* usually buried themselves and came to rest in sand of 37° (the average of 29 trials). The temperature optimal for activity of this lizard and the lethal body temperature do not differ very widely; the former ranges from 35° to over 40°, the latter is 45°–50°.

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COMPARISON OF THE ENVIRONMENT AND SOME PHYSIOLOGICAL RESPONSES OF PRAIRIE VEGETATION AND CULTIVATED MAIZE *

EVAN L. FLORY

University of Nebraska

A survey of the literature reveals that rather numerous studies have been made of the measurements of the environmental factors and the native vegetation of various areas. Representative researches are those of Fuller ('14) on the sand dunes about Lake Michigan, Weaver ('17) in Washington and Idaho, Shreve ('15) on the deserts and mountains of Arizona, Clements and Weaver ('24) in the several plant associations between the Missouri River and the Rocky Mountains, and Whitfield ('33) in the Rocky Mountains. Relatively few similar researches have been pursued in cultivated vegetation. The studies by Kiesselbach ('16), Weaver and Bruner ('27), Vestal and Bell ('31), and Aikman ('31) are examples of such analyses in cultivated fields. No studies, so far as the writer is aware, have been made with the purpose of determining and comparing the environmental factors or the physiological responses of native vegetation and cultivated crops.

Comparisons between native and cultural vegetation are rapidly becoming increasingly difficult since some of the remaining natural areas are each year being grazed, or broken and planted to farm crops. Continued cropping is presenting perplexing problems concerning soil structure and fertility, erosion by wind and water, and maintenance of organic matter. The severity of hot winds and dust storms is also probably increasing due to the laying bare of vast areas in the agricultural practices of producing annual crops. Numerous other environmental changes have occurred.

OBJECTIVES AND PROCEDURE

This study deals with a comprehensive comparison of the environment and certain physiological responses of native prairie vegetation and cultivated corn. Environmental factors were quantitatively determined for the three growing seasons 1931 to 1933, inclusive. They included atmospheric factors of precipitation, humidity, temperature, wind, evaporation, and light. Mechanical analyses of the soils were made and their hygroscopic coefficients, volume weights, and water-holding capacity were determined. Continuous records of soil temperature were obtained; water content was determined weekly to a depth of four feet; the rate of percolation was ascertained; and run-off and erosion were measured in 1933. The physiological responses measured were

* Contribution from the Department of Botany, University of Nebraska, No. 98.

rate of water loss, rate of growth as determined by increase in height and leaf surface, and production of dry matter.

LOCATION OF STATIONS

This investigation was pursued in the Belmont prairie, three and one-half miles due north of the State Capitol in Lincoln, Nebraska. The topography is moderately rolling. The elevation is 1,200 feet, which is about 60 feet higher than the general level of Salt Creek Valley which lies 1.5 miles south. The stations were located about twenty rods north of the crest of a broad, flat hilltop about 40 acres in extent. The slope northward from the crest varied between one and five per cent. The prairie station was toward the northern end of more than 160 acres of native grassland which had been disturbed only by mowing. An area about 30 rods wide and 80 rods long in the northwest portion of the prairie had been broken and cropped in corn for three consecutive years previous to the beginning of the experiment.

In studying the environment of a single habitat, it is necessary to eliminate, so far as possible, the influences of surrounding habitats. Prevailing winds, unless they blow over a broad expanse of a given habitat, profoundly affect the normal temperature, humidity, and rate of evaporation. The station in the cornfield was located approximately 250 feet from the east side of the field. The prevailing southwest wind swept over about one-fourth mile of cornfields before reaching the station. The prairie station bordered the cornfield on the east (fig. 1). It was far enough from the field, however, so that the

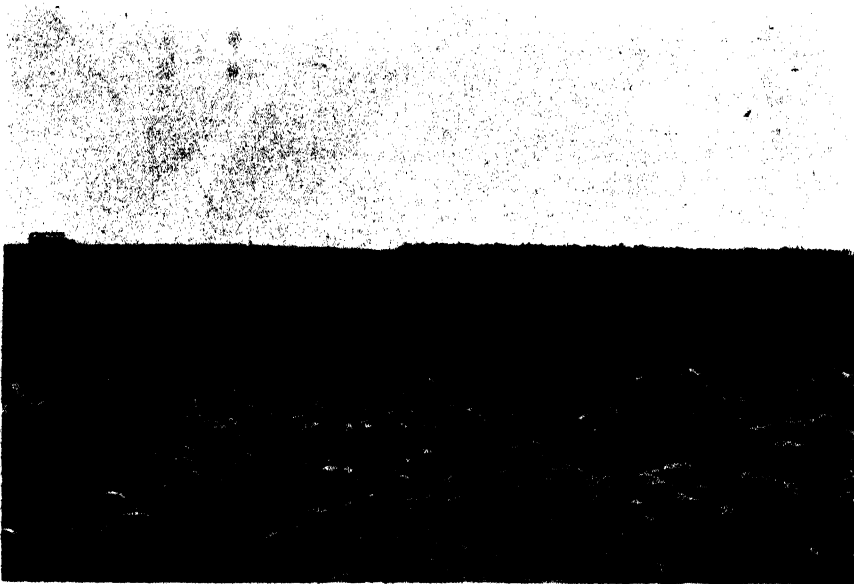


FIG. 1. General view, looking southward, of the cornfield and prairie. The stations are at the extreme right and left of the area included in the photograph. The small area of prairie on the right lies in an unbroken ravine and interrupts the continuity of the field of maize. Photo. July 6, 1933.

prevailing winds blew over nearly one-half mile of prairie before reaching the instruments and plants at this station. A careful check of all the factors showed that each station was in a position representative of its habitat. The stations, however, were in sufficient proximity to each other so that slope, soil, and rainfall were practically identical.

SOIL

The fairly mature upland soil of this rolling topography is known as Lancaster loam. It is derived from the Dakota sandstone formation. The **A** horizon extends to a depth of about 16 inches; the **B** horizon lies between 18 and 30 inches; and the **C** horizon extends beyond the depth of the roots of the grasses. The surface layer is a very dark grayish brown loam about 12 inches in depth. It is thoroughly interlaced with grass roots, has a high organic content, and is of excellent granular structure. Noticeable amounts of fine sand make it very friable. A transition layer lies between 12 and 16 inches. It is grayish brown and friable and increases in compaction and clay content. The structural aggregates increase in size up to 2 to 3 mm. The zone of clay accumulation extends from 16 inches to a depth of 30 inches. The soil is friable, light grayish brown in color and occasionally shows rusty brown iron stains. The granules are 3 to 4 mm. in diameter. The grass roots are numerous but small.

The texture becomes much sandier below 30 inches. There is little change in color except that rust stains and chalky spots are numerous. The sand content increases to a depth of about 42 inches. The sand is rusty brown in color between 42 and 44 inches. At greater depths it is cemented and compact.

The hygroscopic coefficients, as determined by the Hilgard method, show the similarity of the soils in the two sections (table I). Volume weight is the

TABLE I. *Volume weights and hygroscopic coefficients of the soils in the two habitats to a depth of 4 feet*

Depth, inches	Prairie		Cornfield	
	Volume weight	Hygroscopic coefficient	Volume weight	Hygroscopic coefficient
0-6	1.12	7.4	1.30	6.8
6-12	1.31	7.9	1.37	6.7
12-24	1.41	8.1	1.49	6.7
24-36	1.59	6.8	1.55	7.4
36-48	1.57	6.6	1.64	5.7

ratio of the water free weight of the soil, expressed in grams, to the volume which the soil occupies, expressed in cubic centimeters. It was determined by obtaining the dry weight of an undisturbed cylindrical core of soil 4 inches in diameter and either 6 or 12 inches in length. The higher volume weights in

the cornfield show a slight tendency of the soil to become more compact under cultivation.

NATURAL VEGETATION

The vegetation is of the upland, tall-grass type. It has been fully described so recently by Weaver and Fitzpatrick ('34) that only a summary statement need be given here. The little bluestem, *Andropogon scoparius*, constitutes about 60 per cent of the entire cover of vegetation. The basal or ground cover is about 15 per cent. The foliage cover, which varies greatly from year to year and with the progress of the season, is usually between 75 and 100 per cent (fig. 2). *Stipa spartea*, *Koeleria cristata*, and *Sporobolus heterolepis* are bunch-grass associates, and small amounts of the sod-forming *Andropogon furcatus*, *Sorghastrum nutans*, and *Poa pratensis* occur. The forbs consist mostly of legumes, chief of which are *Amorpha canescens*, *Astragalus crassicaupus*, and species of *Petalostemon* and *Psoralea*, and of composites such as *Helianthus rigidus*, *Antennaria campestris*, *Erigeron ramosus*, *Echinacea pallida*, and several species of *Solidago*. Numerous other species occur, but everywhere the grasses are dominant.

The vegetation comprises three principal layers, little bluestem being the chief component of the middle one (fig. 3). The overlapping leaves of the various layers may actually give the surface more than one complete foliage cover thus reducing light intensities at the soil surface to only 3 to 8 per cent. Each species has adjusted itself to endure the conditions imposed upon it by the dominants or to profit by association with its neighbors. Competition for the factors—the needs of life—has resulted in successive crops of various species from early spring until late fall. The various factors of the habitat are thus more fully utilized.

The plants absorb their water and nutrients from different soil levels. Root habits of plants are so stable that species may be grouped according to the soil level or levels they occupy. Plants occurring on a single square meter of soil surface often absorb water and nutrients from three or more cubic meters of soil. Roots of *Koeleria cristata* absorb to a general depth of about 1.5 feet, *Andropogon scoparius* to 4–5 feet, while *Aster multiflorus* and *Amorpha canescens* penetrate to about 7 and 12–16 feet, respectively (Weaver, '19).

The segregation of root systems and underground parts into more or less distinct zones results in a somewhat complementary relationship between the different species below the soil surface. The soil is well occupied everywhere, from about one-half inch below the surface to several feet in depth, by the slender, fibrous roots of grasses and various other types of root systems. The surface soil contains a network of rootstocks, and various other underground plant structures. Hence, invaders are unable to gain a foothold in the apparently bare areas between plants or plant clumps. An excellent condition of tilth results from this community habit. The soil rarely cracks and exposes extensive surfaces to evaporation as it often does under cultivation.

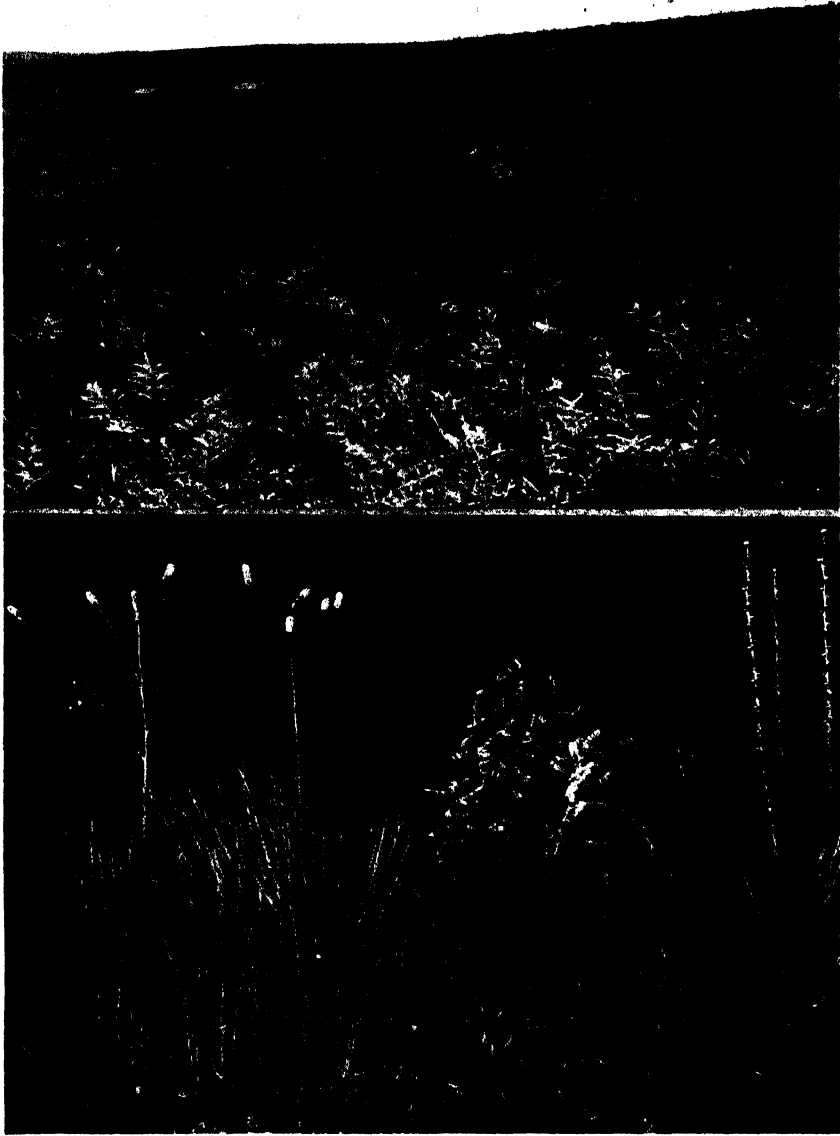


FIG. 2. (Above.) Station in the prairie. The most important grass is *Andropogon scoparius*. At this time, July 6, *Amorpha canescens* was in full bloom and very conspicuous.

FIG. 3. Layers in the little bluestem, upland prairie. Ground layer; rosettes of *Antennaria campestris*; *Andropogon scoparius* (16 inches high) constitutes the main or middle layer; the top layer consists of *Petalostemon candidus* (left), *Amorpha canescens* (center), and *Liatrus scariosa* (right). Photo. Aug. 5. (After Weaver.)

THE FIELD OF MAIZE

Krug yellow dent corn was drilled with a lister in rows 42 inches apart, the plants being spaced about 22 inches in the row. Three cultivations were sufficient to keep the field free of weeds. The first was made when the corn was 5 inches high. It consisted of removing a small amount of soil from the edges of the furrows and placing it about the young plants. The second cultivation, when the corn was about 12 inches high, leveled the surface by throwing the ridges on each side of the row of corn into the furrow. During the last cultivation, about July 10, the soil was thrown into ridges about the base of the stalks. After settling, the soil in the rows was about three inches higher than that between them.

AMOUNT AND NATURE OF PRECIPITATION

The mean annual precipitation at Lincoln, over a period of 56 years, is 27.79 inches. Its distribution is of the Great Plains type, approximately 79 per cent occurring between April 1 and September 30. Forty-six per cent occurs between May 1 and July 31. This seasonal distribution of moisture is very favorable to the growth of native as well as cultivated grasses. Summer rains occur largely as thundershowers with a heavy precipitation falling in a short time. Over one-half of the rainfall in May, June, and July consists of storms of more than an inch in 24 hours. This type of precipitation results in considerable run-off and surface erosion. Sixty to sixty-five per cent of the rainfall occurs at night, hence the amount of water lost by evaporation is reduced. Drought periods of two or more weeks duration occur every season. These consist of periods when rainfall on consecutive days does not exceed .20 inch. Such rains are of little, if any, value in increasing the water content of soil, although they tend to lower temporarily the temperature and increase humidity.

RUN-OFF

Heavy rainfall is of little benefit to vegetation unless the water is absorbed by the soil. Water allowed to run away is not only lost to the plant but also it carries with it solutes and organic matter which greatly affect tilth and water-holding capacity of the soil.

Interceptometers were installed, one in the prairie and one in the adjacent cornfield, where the slope was 5 per cent, on July 15, 1933. They consisted of heavy galvanized iron tanks three feet long, 8 inches wide, and 16 inches deep. Each had a sloping roof, constructed in such a manner that no water could enter the tank except that running down the hill. The 3-foot front of the tank was closely fitted to the upper side of an excavation just large enough to receive it. It was firmly wedged against the undisturbed soil so that all water running down the slope would enter it. Ditches were dug 30 feet farther up the slope so as to divert the run-off water from still higher areas away from the interceptometer. Hence, the tank received only the run-off

from the area thirty feet long immediately above it. The interceptometer in the cornfield was located between two rows of corn, a ditch 30 feet above it diverting the water between adjacent rows.

A gentle rain totaling 0.59 inch fell on August 8, during a period of six hours, following two weeks of drought. There was no run-off at either station. A rain of 1.92 inches fell during a period of two hours on September 9, the first 0.79 inch falling in 20 minutes. One per cent of the water that fell on the prairie ran away carrying with it less than 0.1 per cent solid matter; in the adjoining field the run-off was 60 per cent. The water carried with it a load of over 10 per cent solid matter. Twenty-one similar rains falling upon the cultivated field would have removed the surface inch of soil. There were at least three other rains as effective as the one described during the summer of 1933 alone. In addition there were other lighter showers during the summer months, and periods of rainfall during the remainder of the year that eroded the soil.

The excessive run-off in the cornfield resulted partly from the clogging of the pores at the surface of the bare soil by suspended material. Raindrops beating upon a bare soil break up the soil aggregates into finer particles which move into the spaces between the larger aggregates. This more or less effectively seals the soil and does not permit rapid absorption of water. The prairie soil is protected from this action by a cover of living plants, stubble, and fallen debris. The amount of litter on a square meter is often 225 grams. It can absorb 650 grams of water, which is equivalent to .03 inch of rain. Its main effect, however, arises from its lodgment among the grass stems and stubble where it forms an intricate series of minute dams and terraces which hold much of the water in place until it percolates into the soil.

RATE OF PERCOLATION AND WATER-HOLDING CAPACITY

The excellent granular structure and the organic matter of the prairie soil augments both the rate of percolation and the water-holding capacity. Passageways formed by decay of roots, by the burrowing of worms, ants, and insect larvae, as well as ancient rodent burrows, combine to decrease volume weight, to increase pore space, and to accelerate the rate of percolation.

For determination of the rate of percolation, soil cores were taken with accurately machined brass cylinders, 4 inches in diameter and 6 inches long, thoroughly coated with paraffin to insure intimate contact with the soil. These were forced into the soil by means of an hydraulic jack (Russel and Balutkin, '34). When the tops of the cylinders were even with the soil surface, the soil around the cylinders was removed and the cores of soil were cut smoothly across the base. They were then covered with closely fitting lids and taken to the laboratory where they were placed over funnels in a rack. A water-tight, brass collar, 2 inches in height, was fitted over the top of each cylinder. A constant head of water of about 1 mm. depth was

maintained over each cylinder by means of aspirating siphons until the percolation through each column became constant. When this point was reached the amount of water percolating through the soil in a given time was measured. This was used as a basis for calculating the number of inches of water percolating through the soil per hour (cf. Bouyoucos, '30).

The cylinders were then covered and allowed to stand until the free water had drained away. The water remaining was designated as the water-holding capacity. Its amount was determined by drying the soil at a temperature of 110° C. The pore space is the percentage of the space in the cylinders not occupied by water-free soil. It was 50.5 per cent in the prairie soil and 44.3 per cent in the field.

The rate of percolation in the prairie soil was .94 inch per hour, and in the field soil .54 inch. The water-holding capacity of the two soils was 37.8 and 34.0 per cent respectively. Thus the rate of percolation in the field was 42 per cent less than that in prairie, and the water-holding capacity 10 per cent less.

In another experiment, five cylinders were sunk in the soil of each habitat and the rate of percolation determined without removing the soil. A water-tight collar was attached to the top of each cylinder and 100 cc. of water was added. The time required for it to seep into the soil was noted. As soon as the water disappeared from the surface, another 100 cc. portion was added until the rate of percolation became constant. This required about 800 cc. in both field and prairie. At this point the time required for the subsequent 100 cc. portions to percolate into the ground was 20 minutes in the cultivated soil but only 11.6 minutes in the prairie. This experiment gave the time of percolation 72.4 per cent longer in field than in prairie.

DISCUSSION

Bringing soils under cultivation results in a series of changes. Plants are usually removed instead of being allowed to decay where they grew, while temperature, moisture, and aeration relations are altered, and micro-organic life is thrown out of balance. Under cultivation, except in arid regions, decomposition of organic matter may exceed its formation. In general, the results of various investigators indicate that cropping and cultivation are very destructive to the organic matter and nitrogen of the surface soil.

Russel ('29) reported on studies of organic matter made in 67 fields from various parts of Nebraska. He found that nine fields under cultivation for a period of 7 years lost 6.5 per cent of their original organic matter, and twelve fields under cultivation between 45 and 60 years had an average loss of 28 per cent. Fifteen fields under cultivation 30 to 60 years and subject to erosion lost 56 per cent of their original organic matter. Loss of organic matter in all these cases was based on a comparison of the analysis of the top foot of the cultivated soil with comparable adjacent virgin lands.

Organic matter influences structure, increases aeration, facilitates drainage, improves tilth, and increases water-holding capacity. It checks erosion and causes more rapid warming of the soil in spring. It has a buffer effect which helps to regulate soil reaction. It furnishes energy materials to hordes of microorganisms. The number of microorganisms and their activities may increase the supply of organic residues. Therefore the maintenance of organic matter is of great importance (cf. Reuszer, '31).

Rate of erosion, under an average precipitation of 36 inches, has been ascertained at the Missouri Agricultural Experiment Station over a period of six years (Duley, '24). Run-off and surface erosion were compared on similar slopes of 3.68 per cent. One field was plowed four inches deep and the other was in grass. Losses by run-off from the plowed field equaled 31 per cent of the rainfall. In the grassland losses were 11.5 per cent. The field lost its top soil at the rate of 7 inches in 24 years. The removal of a similar amount of soil from the prairie would require over 3,500 years.

The importance of a plant cover in checking run-off and erosion is shown by the studies of Forsling ('31). He states that "the increase in the density of the vegetation from 16 to 40 per cent of a complete cover and the replacement of certain plants by others with more extensive and more fibrous root systems reduced the rainfall surface run-off 64 per cent and rainfall erosion 54 per cent."

The reduction of the rate of penetration of water of 42 or more per cent during a period of only 6 years of cultivation at Lincoln is significant. The practice of making lister furrows with the slopes, rather than at right angles to them, further aids run-off and surface erosion. Not uncommonly these furrows are farther deepened by erosion on the slopes and filled with the eroded soil in the depressions before the corn has grown to a sufficient height to warrant their being filled again with soil.

PRECIPITATION IN RELATION TO WATER CONTENT OF SOIL

Rainfall was measured by means of a standard rain gauge installed at the prairie station, with its top well above the surrounding vegetation. Precipitation varied widely from year to year both in amount and distribution. The years 1931 and 1932 were characterized by a plentiful supply of rain in June, a shortage in July, a fair supply early in August, and a deficiency late in August. There were four weekly periods in 1931 with no rain, but only one in 1932; moreover, total precipitation for the growing season was much greater in 1932. The year 1933 was characterized by a dry June, much rainfall in July, drought during August, and an abundance of moisture in September.

The available water content showed a wide variation from year to year as a result of the variation in precipitation. The seasons of 1931 and 1932 were similar in that during the early part of June there was a plentiful supply of available water. In 1931 the supply exceeded 20 per cent in each habitat

in the surface 6 inches of soil and 10 per cent in the fourth foot. The amount was about 5 per cent less in both the surface 6 inches and the four-foot level, in 1932. The supply was almost depleted in July of each year; restored, except in the lower levels, in August; and largely depleted at the end of the season. Conversely, the season of 1933 began with a small amount of available water which was greatly augmented at all levels in July; practically depleted in August; and again restored by September 11. Thus at the end of the growing season of 1933, the amount of water at all levels was equal to that at the beginning of the season.

A more direct relationship was found between rainfall and available water in the first 6-inch level in the prairie than in the cornfield. Showers of less than .25 inch, however, had more effect on available water in the cornfield. The loose, dry, surface soil in the field readily absorbed the light rains. The increase in available water, however, was greater in the prairie following heavy rains. If one-half inch of rain fell during a period of an hour or less, there was appreciably more run-off in the field. This difference of water content increased with an increase in the rate of rainfall.

AVAILABLE WATER CONTENT IN PRAIRIE AND CORNFIELD

Available water in the surface 6 inches was 12.5 per cent in the prairie and 15.3 per cent in the cornfield at the end of the first week in June, 1932 (fig. 5). An average of slightly over 1.5 inches of precipitation per week fell during the following three weeks. It increased the available water in the prairie to 15 per cent, but there was no accompanying increase in the cornfield. The increase in the prairie occurred notwithstanding the fact that the grassland was losing an average of about two pounds of water per square foot of soil surface per day. The corn, which was only about six inches high, was not yet using water in large quantities, but water was being rapidly lost by evaporation from the almost bare soil surface. The furrows in the listed field, moreover, furnished ideal channels for run-off.

Heavy rains usually increased the available water in the prairie more than in the field, because of greater run-off in the latter. During periods of drought, however, the available water in the prairie was depleted more than that in the field. Available water in the surface 6 inches on July 18, 1932, was 0.6 per cent in the prairie and 4.2 per cent in the field when the corn had reached a height of 5 feet. A rain of 2 inches during the following week increased the available water in the prairie to 8.9 per cent and in the cornfield to 8.3 per cent. The actual increases were 8.3 and 4.1 per cent in the prairie and field, respectively. The available water was completely exhausted in the surface 6-inch level of the prairie once in 1932 (fig. 5), and once in August 1933 (fig. 6). Less than one per cent remained during the drought in September 1931 (fig. 4), and in June, 1933 (fig. 6). The water in this layer was completely exhausted in the cornfield only once during the three years.

Available water in the second 6-inch level was practically depleted in the grassland in July and completely exhausted in September, 1931 (fig. 4). The lowest point reached in the cornfield at either of these periods was about 5 per cent. Water in the second six-inch layer was not exhausted in either habitat in 1932 because of more even distribution of rainfall. Only one week

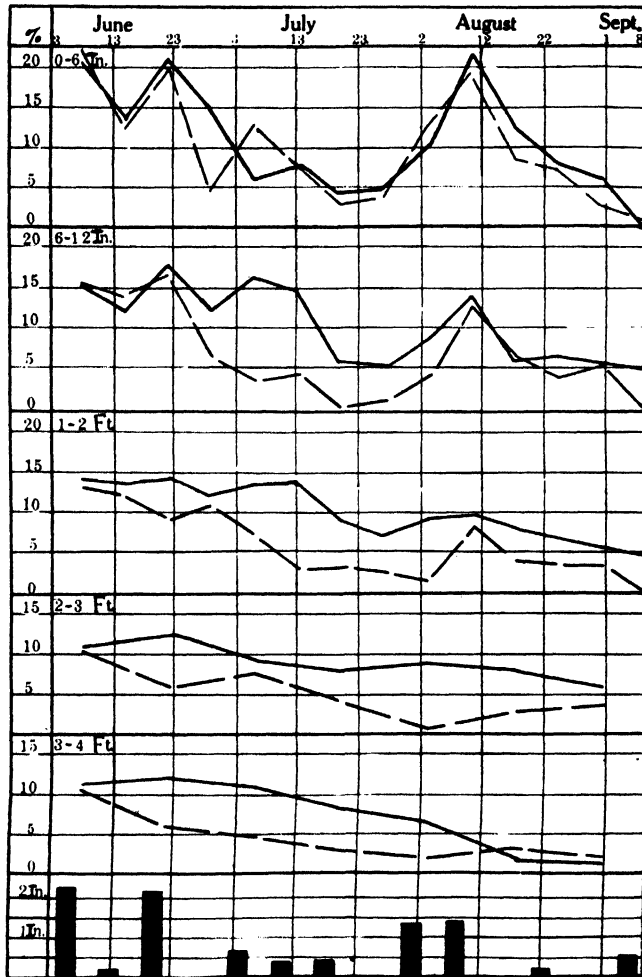


FIG. 4. Percentage of available water at the several depths to four feet in the prairie (broken lines) and in the cornfield (solid lines), 1931; also weekly precipitation in inches.

during the summer was without precipitation (fig. 5). In 1933, two periods of drought, each extending over more than two weeks, were responsible for almost complete exhaustion of available water (fig. 6). The relationship between rainfall and water content in the second 6-inch level was closer in the prairie than in the field, but it was not as pronounced as in the surface layer.

Water content in the second foot was continuously lower in the prairie than in the field, with two exceptions in 1933, following very heavy rains during which run-off in the field was much greater than in the prairie (fig. 6).

The relation between rainfall and available water was still perceptible in

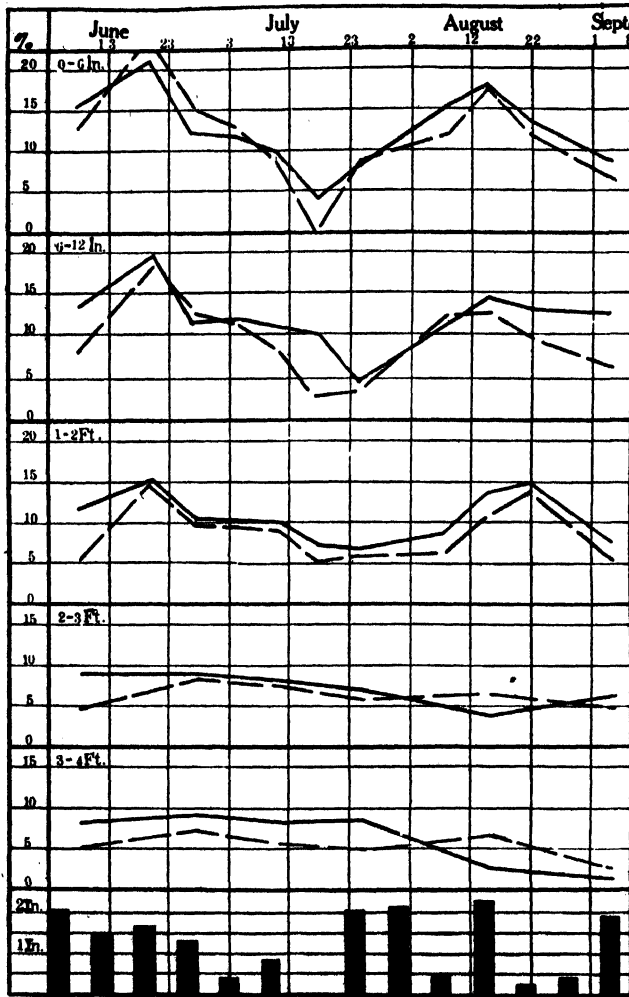


FIG. 5. Percentage of available water at the several depths to four feet, 1932. As in the following figures, unless otherwise indicated, the solid line shows the factor in the cornfield and the broken line in the prairie; also, weekly precipitation in inches, below.

the third and the fourth foot. The prairie soil continued to show the closer relationship. The heavy demands of corn for water during the middle of August at the time of "shooting," reduced the available moisture in the fourth foot during each of the three years below that in the prairie (figs. 4, 5, and 6). The failure of the corn to reduce the moisture in the third-foot level in 1931, as it did in the fourth-foot, was obviously due to the penetration of moisture only into the third foot. The corn roots, however, vigorously ab-

sorbed at both levels. They probably did not penetrate beyond 4 feet in the cemented sandy subsoil.

Corn made slight demands upon soil moisture until the latter part of June, hence it would seem that an appreciable amount of water should have accu-

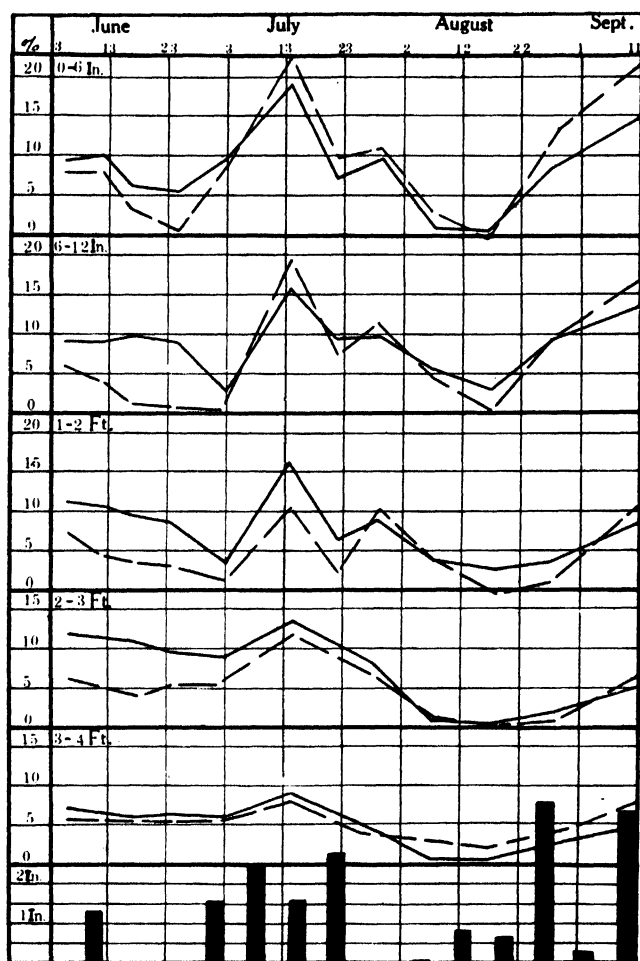


FIG. 6. Percentage of available water at the several depths to four feet, 1933; also weekly precipitation in inches.

mulated in the soil during early summer. Actually there was not much more water in the field than in the prairie where vegetation had been growing vigorously for a period of 10 weeks. The bare, compact soil in the cornfield did not favor either the penetration or the retention of water. After the new crop was planted the ridges made by the lister exposed a large surface to evaporation and the furrows running down the hill greatly facilitated run-off. Stirring the surface soil by cultivation and the late demands for water by the growing crop were, on the other hand, conducive to more available moisture in the cornfield.

RELATION BETWEEN PRECIPITATION AND PRODUCTION OF DRY MATTER

The direct relation between the production of dry matter in prairie and cornfield and the mean monthly rainfall is shown in table II.

TABLE II. *Mean monthly production of dry matter in prairie and in field in relation to mean monthly rainfall*

Criteria	April	May	June	July	August	September	Total
Percentage dry matter, prairie	2	26	36	21	13	2	100
Percentage dry matter, corn	—	—	8	42	41	9	100
Percentage of mean annual rainfall . . .	10	16	17	15	13	9	80

The greatest growth occurred during the month of greatest precipitation. During the three years the prairie vegetation made demands upon moisture as rapidly as it was available. There was never any great accumulation over any considerable period of time. An exception resulted from the unusually heavy rains in September, 1933.

DISCUSSION

The prairie usually has an excess of moisture after the demands of the dominants have been met. These marginal supplies account for the diversified structure of the climax vegetation. The utilization of these marginal supplies by secondary and subdominant species makes possible the four distinct seasonal aspects in the prairie, a monthly production of dry matter proportional to the monthly precipitation, and the absence of any great accumulation of available water at any time. The single species and its late development in the cornfield accounts for the early accumulation of available moisture in this habitat. In the same manner the uniform development of corn accounts for the great demand made by corn in the third and fourth foot of soil at the time of shooting. According to Kiesselbach ('16) a single corn plant may transpire 4 to 7 pounds of water during a period of 24 hours when the weather is hot and dry. During all three years the available moisture at these levels was reduced below that of the prairie and practically exhausted.

The dependence of the crop of corn upon a good supply of water and favorable temperatures at this time is well stated by Smith ('20). "When July in Ohio is warm and wet, the probability of the corn yield being greater than average is 85 per cent. When it is cool and wet the probability of a good corn yield is 73 per cent. On the other hand, when July is cool and dry, the probability of a good corn yield is only 38 per cent, and when July is warm and dry it is only 33 per cent. . . . Rainfall for the 10 days after blossoming

has the greatest effect on the yield of corn of any period in the development of the plant."

AIR TEMPERATURE

A temperature range between 50° and 95° F. is necessary for the best development of corn. As the temperature approaches 50° the growth rate of corn decreases rapidly. This effect is perhaps largely due to a slowing of the chemical processes of cell division, but may in part be due to a decreased rate of translocation of food materials at the lower temperatures (Loomis, '34). Temperatures maintained above the optimum result in abnormal development and growth ceases altogether above 118° F. (Wallace and Bressman, '28). Extreme fluctuations in temperature may also prevent maximum plant development.

The data on temperature and humidity were secured by means of Friez' hygrothermographs housed in well ventilated, rain-proof, wooden shelters of the Weather Bureau type. The sensitive portions of the instruments were about 5 inches above the surface of the soil. The instruments were checked frequently but extreme care was exercised at all times to disturb the surrounding vegetation as little as possible. The average day temperatures were secured from the weekly record sheets by adding the temperatures of each 2-hour period from 6:00 A.M. to 6:00 P.M., inclusive and dividing by six. Those for the night, from 6:00 P.M. to 6:00 A.M., inclusive, were calculated in the same manner. Variations not perceptible in the mean day and mean night temperatures were revealed when the maximum or minimum temperatures for each day of the week were averaged.

The average day and average night temperatures in the cornfield were always 1° to 5° higher than in the prairie. The mean temperature for the entire three-year period was 74.5° F. in the prairie and 77.9° in the cornfield. During the day the mean temperature in the prairie was 3.9° lower than in the cornfield, but only 2.7° lower at night. The mean day temperature in the cornfield ranged from 2° to 7° higher than in the prairie. Day temperatures have a marked effect on transpiration since the stomata are usually open during the day, the humidity is lower, and the wind movement is more constant than at night. Since transpiration at night is only 7 to 8 per cent as great as in the daytime, it has been suggested that the weather factors for the day only should be used in studying their effect upon the total transpiration (Kiesselbach, '16). Temperature is an extremely important factor in promoting transpiration. It has been found by Kiesselbach ('16) that a fully grown corn plant will transpire daily about 4 pounds of water at a mean temperature of 70° F., whereas at 80° F. it will transpire about 7 pounds.

The mean daily maxima averaged 3.9° higher in the cornfield with a range of 0° to 9° higher than in prairie. The greatest differences occurred during dry hot periods. Mean daily minima in the field ranged from 5° below those in the prairie to 9° above, with an average of 3.2° above that of

grassland (fig. 7). The average difference between the mean daily maximum and the mean daily minimum temperatures for the three year period was 24.1° in the cornfield and 23.4° in the prairie.

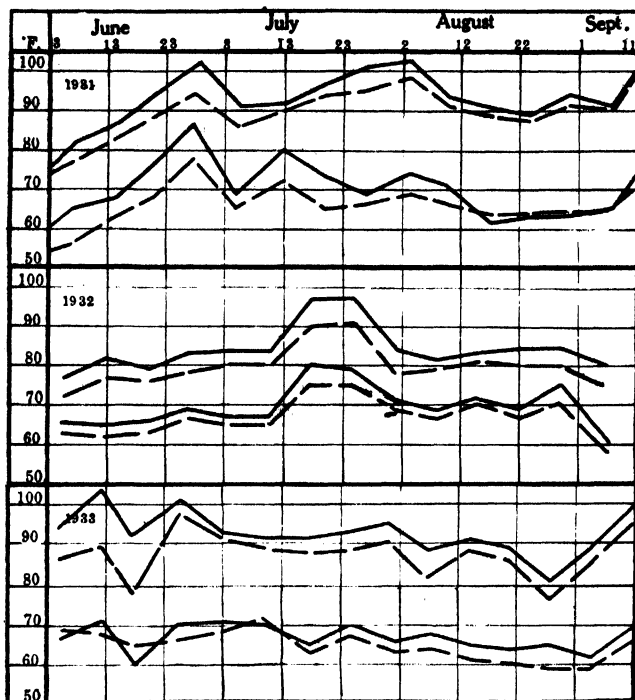


FIG. 7. Average weekly maximum and minimum air temperatures during 1931, 1932, and 1933.

The maximum temperature attained each week was 0° to 11° F. higher in the cornfield than in prairie with a mean 4.8° higher over the entire period. Minimum weekly temperatures in the cornfield ranged from 4° below to 4° above those in the prairie. The mean was 1.7° above.

The mean temperatures were not greatly different in the two habitats during the three years, nor were the differences between mean day and night temperatures or the mean maxima and minima. Extremes, however, were more critical and significant than means.

The stabilizing effect of prairie vegetation, as observed during a two-week period ending July 25, 1933, is typical of the reaction of the prairie upon its habitat during periods of high temperatures, low humidities, and low water content of surface soil (table III).

TABLE III. Average daily temperatures in degrees Fahrenheit for the two-week period ending July 25, 1933

	Cornfield	Prairie
Average day temperature.....	97.0	90.0
Average night temperature.....	79.0	75.0
Mean daily maximum temperature.....	104.0	96.0
Mean daily minimum temperature.....	66.0	70.0

Even though the prairie and cornfield soils contained 6 and 4.2 per cent of available water, respectively, the heavier cover of vegetation of the prairie influenced the habitat to such an extent that the day temperatures averaged 7° less, and the night temperatures 4° less than in the field. The maximum temperature was 8° lower and the minimum 4° higher than in the less stable field habitat. The average daily range between the maximum and the minimum temperatures in the prairie was 26° , as contrasted to 38° in the more open cornfield.

High temperatures were commonly found to be associated with periods of low rainfall and depleted soil moisture. This increased their severity since they lowered the humidity and thus augmented the desiccating effect upon the vegetation.

The differences in temperature in the two habitats were more pronounced early in the season before the corn produced much shade. They were not as great, however, as the difference in cover would indicate, because the somewhat greater accumulation of soil moisture in the cornfield increased the specific heat of the soil. The prairie vegetation had been rapidly transpiring the water from the soil. The early seasonal differences are illustrated by the data for the week ending June 26, 1933, when the corn was about 12 inches high. Day temperatures averaged 3° higher in the cornfield and night temperatures 1° lower than in the prairie. The weather was hot and clear. Available water in the surface 6-inches of soil was 5.3 per cent in the field and 0.8 per cent in the prairie. The average maximum temperatures were 108° F. in the field and 106° in the prairie, and the minimum temperatures were 47° F. and 56° , respectively. The average daily difference between maximum and minimum temperatures was 61° in the field and 50° in the prairie.

Early seasonal differences between temperatures in the two habitats were maintained in part throughout the summer. The tendency of the shading of the growing corn to lessen these differences was partly counteracted by an accompanying increase of the foliage in the prairie.

The stabilizing effect of the prairie habitat on temperature was clearly illustrated by the thermograph records on clear summer days when cumulus clouds shaded the field for periods of 5 to 10 minutes. They show a lowering of temperature in the cornfield but similar slight variations usually did not occur in the prairie (fig. 8).

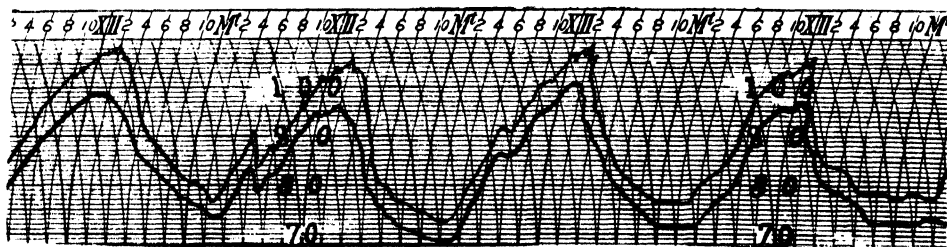


FIG. 8. Portion of thermograph records (transcribed) showing the temperatures in cornfield (upper line) and prairie (lower line) from July 14 to 17, 1932.

HUMIDITY

The mean daily humidity in the prairie and cornfield, for the three-year period, was 71.6 and 69.4 per cent, respectively. Average day and night humidities in the prairie were nearly always intermediate between the average day and average night humidities in the cornfield. The day and night humidities were both higher in the prairie during periods of drought. This was especially noticeable during the drought of July, 1932, and of June, 1933 (fig. 9). The relatively heavy cover of vegetation in the prairie maintained

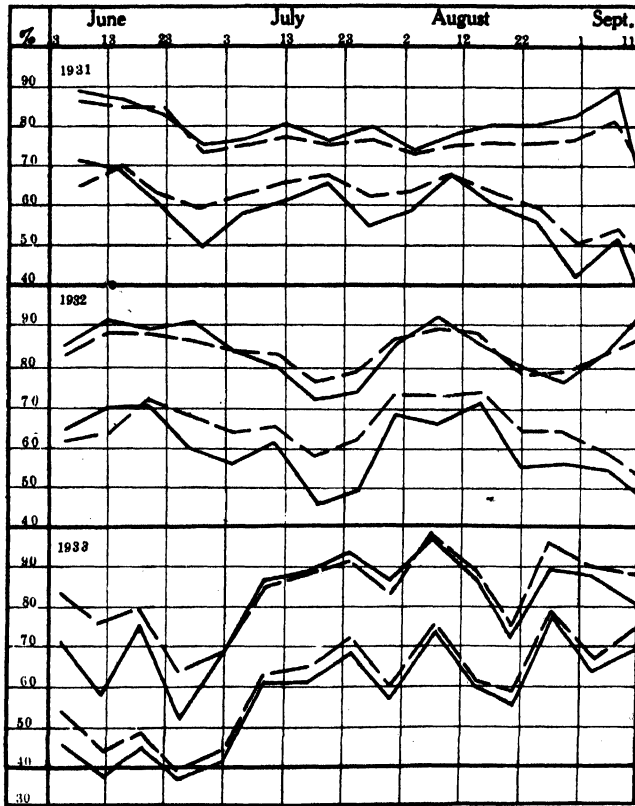


FIG. 9. Average day and average night relative humidities at the two stations during 1931, 1932, and 1933.

lower temperatures and hindered the wind from removing the moist air at the soil surface and around the plants, as it did in the cornfield.

The prairie was decidedly more equable in respect to humidity than was the cornfield. The daily and the weekly maxima were nearly always lower in the field. The average difference between the maximum and the minimum humidities for the three summers was 43.2 per cent in the field but only 34.5 per cent in the prairie. The average daily maximum humidities were lower in the prairie because of less extreme air temperature fluctuations. An ex-

Wind is an important factor, especially dry, continental winds, both in promoting water loss directly from the plant and evaporation from the soil. Since mid-continental winds are practically always dry they remove the humid air immediately surrounding the plant and replace it with drier air, thus facilitating transpiration. Increased transpiration lessens leaf turgidity and hastens stomatal closure with a consequent reduction in photosynthesis.

Wind velocities were obtained from anemometers of the standard Weather Bureau type placed in each habitat and operated at 12 inches above the soil surface.

The wind movement was greater in the cornfield during all three years until the second week of July, after which it was less. At this time the corn had reached a sufficient height to obstruct the wind (fig. 11). Thereafter

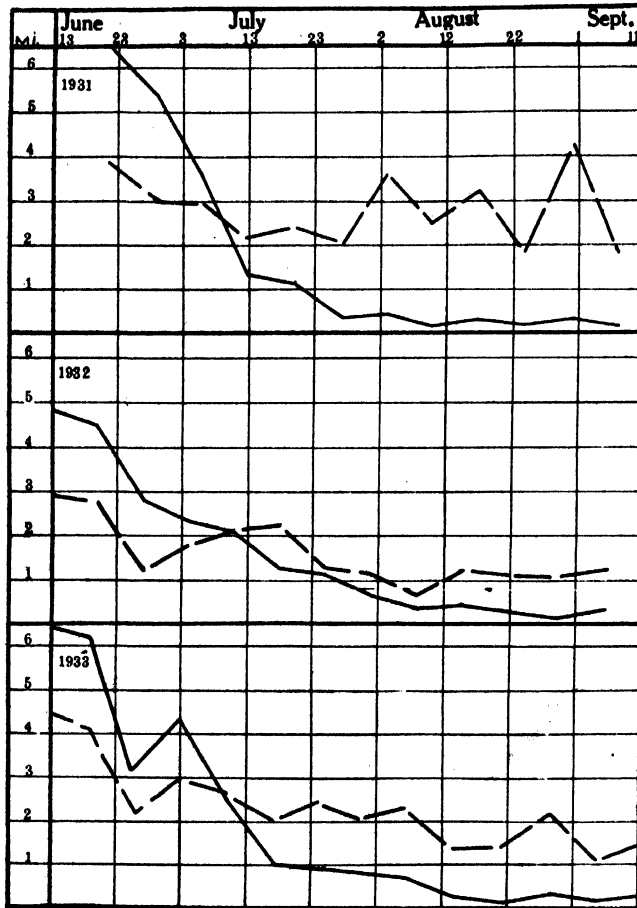


FIG. 11. Average wind velocity in miles per hour at the two stations during 1931, 1932, and 1933.

fluctuations were greater in the prairie, but even high winds had slight effect upon the anemometer in the field. Decreased wind movement, together with the shading in late summer, aided materially in checking evaporation from the soil surface and water loss through transpiration. The shorter, sparser vegetation of both habitats in 1931 accounts for the greater variations in wind movement than during 1932 and 1933.

Prairie vegetation was more effective in protecting the soil surface from wind and consequent loss of moisture than was the field of corn. A series of

readings made with a hand anemometer illustrates the effect of the two types of cover (table IV).

TABLE IV. *Wind velocity in miles per hour at various heights in cornfield and prairie*

July 15, 1932				July 29, 1933			
Height above soil, ft.	Field, corn 44 in. high	Prairie, grass 11 in. high	Increase in prairie, per cent	Place of reading	Field, corn 72 in. high	Prairie, grass 15 in. high	Increase in corn-field, per cent
1	0.6	1.6	166	Soil surface	0.9	0.0	—
2	1.6	3.7	131	Mid-height of plants	2.5	0.1	2400
3	2.4	8.0	233	Top of plants	4.9	3.7	31
4	3.8	8.1	113	3 ft. above plants	8.5	9.1	-6
9	8.5	10.5	22	9 ft. above soil	8.5	9.1	-6

LIGHT

A series of determinations of light intensities were made with Clement's photometers. At the soil surface in the prairie and cornfield, on July 15, they were 5 and 51 per cent, respectively, and at mid-height of the vegetation 24 and 65 per cent.

The shorter, denser foliage cover, with the resulting lower wind movement and lower light intensities, accounts for the greater stability of the prairie environment as was shown by the extremes of every factor being nearer together in the prairie than in the cornfield.

EVAPORATION

The rate of evaporation integrates in a general way the factors of humidity, wind movement, and temperature. Livingston's standardized, white, spherical, porous cup atmometers, fitted with non-absorbing devices, were used. They were operated in pairs at each station at a uniform height of 4 inches. All readings were reduced to those of the standard atmometers. The data for the three years are shown graphically in figure 12.

Fluctuations of evaporation became less pronounced in each habitat as the season advanced due to the stabilizing effect of the increased cover of vegetation. The fluctuations were never as extreme in the prairie as in cultivated land because of the relatively denser cover. They were greatest early in summer. During the week ending June 12, 1933, for example, the temperature in the field averaged 88° F., and in the prairie 83°; the accompanying relative humidities were 48 and 60 per cent, respectively. These extreme conditions resulted in an average daily evaporation of 81 cc. in the cornfield and 56 cc. in the prairie. This was 31 per cent less in the grassland.

The graphs of evaporation in the cornfield approached those of the prairie as the season advanced until the latter part of July, when the corn attained its maximum leaf area (fig. 12). For the remainder of the season the graphs were more or less parallel and differences were not great until the prairie

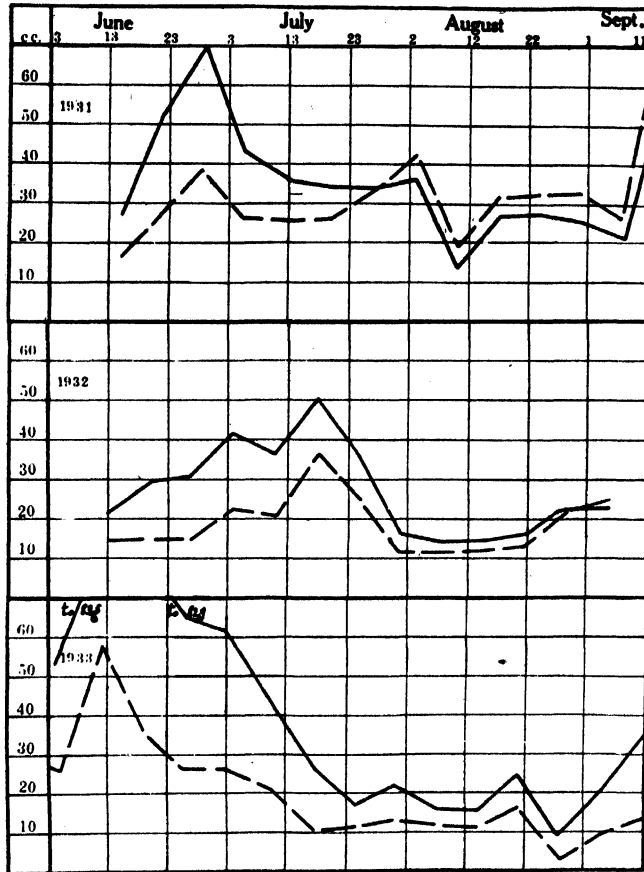


FIG. 12. Average daily evaporation by weeks at the two stations during three growing seasons.

cover was removed by mowing. The prairie was mowed about July 25, in 1931, and evaporation increased beyond that in the field during the remainder of the season. Similar differences occurred in 1932, when it was mowed late in August. The prairie was not mowed in 1933, and in it evaporation was less throughout the entire season.

SOIL TEMPERATURE

Soil temperatures were secured by means of Friez' soil thermographs. The tubes were placed horizontally 3 and 8 inches, respectively, below the soil surface in each habitat, with a minimum of disturbance to the plant cover.

Soil temperatures were always higher in the cornfield than in the prairie;

the mean temperature at 3 inches depth for the three-year period was 8.2° F. higher; the day temperature 8.3° , and the night temperature 8.0° higher in the field. At 8 inches depth, the mean temperature in the cornfield for 1931 and 1932 was 2.2° F. higher, the day temperature 2.4° , and the night temperature 2.0° higher, respectively, than in the prairie.

The range between the average daily maxima and minima, for the 3-year period at the 3-inch depth, was 12.3° F. in the cornfield and 11.5° in the prairie. At the 8-inch depth (1931 and 1932) it was 4.2° in the cornfield and 3.8° in the prairie.

Soil thermograph records in figure 13 illustrate the normal midsummer

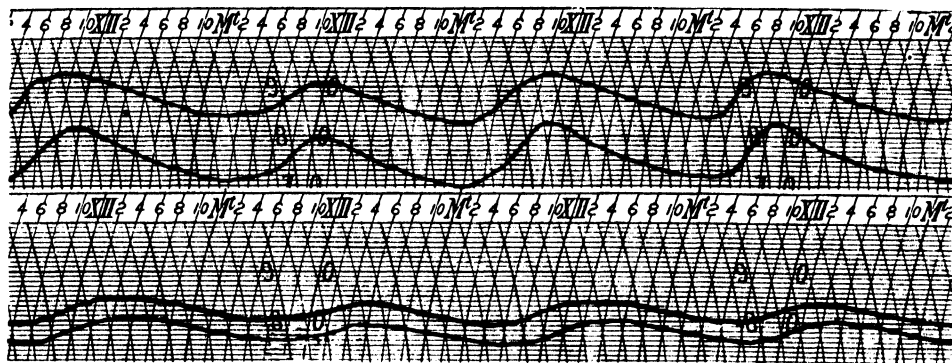


FIG. 13. Portions of soil thermograph records (transcribed) from July 14 to 17, 1932, inclusive. Upper chart at depth of 3 inches, lower chart at depth of 8 inches. The upper line in each record is from the cornfield and the lower one from the prairie.

differences in soil temperature in the two habitats. The graphs at each depth in the field show a consistent relationship to those in the prairie. The differences varied but little from day to day. Maximum and minimum soil temperatures in the prairie, however, lagged almost an hour behind those in the cornfield, due to the denser plant cover. The actual gain of heat in the soil under the cover of grass was much less than that of the comparatively more open field. The living cover of vegetation and the organic debris on the soil in the prairie protect it from direct insolation. The temperature near the soil was relatively lower during the day on account of the great amount of transpiration. At night the still, moist air acted as a very poor conductor of heat. Hence, the soil cooled slower than in the cornfield where there was appreciable air movement near the surface.

The higher water content in the field tended to keep the difference in temperature between the two habitats from becoming greater early in the season. The heat consumed in evaporation of water was at the expense of the heat used in warming the soil. Specific heat of the soil is, moreover, greatly increased by a high water content.

Temperatures of air and soil were compared during one of the most severe

periods of high temperature, low humidity, and drought in the surface soil, on June 10, 1933 (table V).

TABLE V. *Temperatures in cornfield and prairie in degrees Fahrenheit on June 10, 1933*

Place of reading	Cornfield	Prairie	Difference
Air, 4 ft.....	107	102	5
Air, 4 in.....	110	100	10
Surface.....	124	103	21
Soil, 3 in.....	136	99	37
Soil, 12 in.....	84	81	3

The very slow development of corn during these 20 days of intense heat, showed that the high temperatures were above the optimum for its best growth. During the period water was available at a depth of a few inches below the soil surface.

An additional harmful effect of extremely high soil temperatures is that on nitrogen fixation. Russel, *et al.* ('25) have shown that the production of nitrates in eastern Nebraska proceeds at a maximum rate in moist prairie soils at about 94° F. At higher temperatures it becomes slower and at 131° may cease. Thus the growing crop may be deprived of a sufficient supply of nitrates, so far as production in the hot, dry surface soil is concerned. Indeed, even the roots in this layer may wither and die.

Differences in soil temperature in the two habitats did not change appreciably later in the season because shading in the cornfield was not sufficient to lower greatly the temperature. The larger, more leafy plants, however, held the heated air more or less in place. The heavier cover of vegetation in the prairie also tended to blanket further the prairie soil and counteract radiation at night.

DISCUSSION

The relatively heavy cover of prairie grasses protects the soil from direct insolation and diminishes the amount of heat received. It also retards radiation from the soil and thus reduces loss of heat. During the long days of summer the soil receives more heat than it loses by radiation during the short nights. The first effect of the grass cover is the more pronounced, and the actual daily gain of heat in a prairie soil is much less than is the gain in the open. The soil and air temperatures in the prairie are consequently lower and not subject to as extreme fluctuations as in the more open cornfield. In the cornfield the temperatures of the soil surface are higher than those of the air, but in the prairie they are lower than the enveloping air.

Investigators are in agreement as to the effect of cover on the various factors. Data for grassland, however, are scarce since most of the studies have been made in forests.

Toumey and Neethling ('24) showed that from April to October the soil temperature is lower under both living and dead tree cover than when the

soil is bare, the difference depending directly on the density of the living cover and the depth of the litter.

Bouyoucos ('16) reported that minimum temperatures in bare soil at three inches depth, for the three winter months, were 9 per cent lower than in sod.

Craig ('00) found that the minimum temperature at 6 inches depth, after hard freezing in January, was two degrees higher in the sod than in bare soil.

Li ('26) showed that in summer a denuded area was warmest, a grass area intermediate, and a forest coolest.

During the three summers at Lincoln, the average temperature range was 1.2° F. less in the prairie than in the cornfield. Climax vegetation has not only adjusted itself to the extremes of climate, but also it tends to draw the extremes closer together than does a cultivated crop of corn. During periods of drought lasting for two weeks, it was not uncommon for the average daily range between maximum and minimum temperatures in the prairie to be 12° F. less than in the field.

The cover of vegetation in the prairie maintains a uniformly higher relative humidity than is maintained in the adjacent cornfield. This is due to the lower temperature and also to the greater amount of moisture available for evaporation and transpiration. The stabilizing effect of prairie vegetation on humidity is most pronounced when the extremes are most widely separated as in times of drought.

Wind movement is present among the corn plants at all levels but in the prairie it is reduced to nil near the soil surface after the cover of vegetation is well developed. This condition has a decided effect upon the temperature, humidity, and resultant evaporation in the two habitats. The absence of air movement in the prairie aids materially in stabilizing conditions of temperature and humidity.

The rate of evaporation is an integration of the effects of humidity, wind movement, and temperature. It is therefore stabilized largely as these factors are stabilized by the prairie habitat and maintained at a uniformly lower rate.

LEAF AREAS

Determinations of the total leaf area per square foot of soil were made at 10-day intervals in both prairie and cornfield from April until September. The vegetation from four separate areas of one square foot each was taken at each sampling, new soil areas being used each time. In the cornfield, the number of square feet occupied by a single plant was ascertained and the leaf area at each sampling was calculated from a group of representative plants. A wire frame, one square foot in area, was used in the prairie in delimiting the several small areas to be cut at each interval for the determination of leaf areas. The areas were selected at random from typical, dense, little blue-stem sod, which was practically free from forbs, as were also the sods in the phytometers used for determining water loss. When the frame was

placed close to the ground and the vegetation originating within the area carefully separated from that growing without, the grasses were clipped at the soil surface. Care was taken to secure all of the leaves, after which the old, dried leaves were separated from the fresh green ones.

The grasses were cut early in the morning while wet with dew or after a shower of sufficient duration to allow the leaves to become turgid. This prevented shrinking and folding of the leaves. During drought, the areas for cutting were selected the previous evening, well watered, and cut early the following morning. At the time of cutting, the leaves were carefully arranged with their tips all at one end. The bundles of leaves were wrapped in soft, wet paper and then covered with waxed paper until taken to the laboratory. Here the grass blades from the four samples were thoroughly mixed by rolling them lightly back and forth over wet paper. The grass was then weighed and one-fourth of it, by weight, selected as representative of a typical square foot. Care was taken to include in the sample one-fourth of the leaves of any forbs which were intermixed with those of the grasses. The remaining vegetation from the three square feet was used to determine the dry weight.

The leaves of the sample were sorted into as many groups as there were distinct leaf sizes. This was usually about seven. Ten leaves were taken at random from each group and blue prints of them were made. The outlines of the prints were traced by a planimeter in determining the area. The average area of the ten leaves from each group was multiplied by the total number of leaves in the group. The areas of leaves of small forbs, which had been determined separately, were added to the total areas of all the groups. The total area was then multiplied by two, since both sides of the leaves received light and transpired. The product gave the total leaf surface, in square inches, of one square foot of prairie vegetation.

The areas of immature leaves of the corn plants were determined by making blue prints of each leaf as was done with the grasses. The area of mature leaves was ascertained by multiplying the product of the length and greatest width in inches by 1.5 (Montgomery, '11).

Since *Andropogon scoparius* constituted 60 to 70 per cent of the cover of prairie vegetation, and in the selected areas and phytometers over 85 per cent, it was used as representative of the entire plant cover.

Intermixed with it, however, were small amounts of *Stipa spartea*, *Koeleria cristata*, and *Poa pratensis*, all of which made a somewhat earlier growth. Growth of the dominant was resumed about April 15, and by the first of June the stems had about 4 leaves each and the general level of the foliage was 11 inches (table VI).

Prairie vegetation adjusted itself to the rigors of climate. During periods of drought many leaves rolled tightly and exposed the least possible surface. If the drought continued, the leaves at the base of the stem withered and those of the grasses dried at the tips. If conditions favorable to growth

TABLE VI. *Development of the foliage cover in the two habitats during 1933; leaf surface is per square foot of soil.*

Date	Andropogon scoparius		All species	Corn	
	Height, inches	Number of leaves	Leaf surface, sq. in.	Height, inches	Leaf surface, sq. in.
April 26.....	1.0	1	40		
May 3.....	3.2	1	—		
May 10.....	5.1	2	110		
May 17.....	5.9	3	—		
May 24.....	7.6	4	—		
June 1.....	10.8	4	485	Planted	
June 8.....	11.5	4	800	4	—
June 22.....	12.2	4	856	11	46
June 30.....	12.6	5	823	16	110
July 15.....	12.9	5	909	31	318
July 22.....	13.0	6	1003	42	420
Aug. 7.....	23.4	6	981	60	480
Aug. 14.....	36.0	6	963	66	472
Aug. 21.....	44.0	6	952	69	418
Sept. 4.....	45.0	6	948	72	370

recurred before the grass was mature, it again increased its leaf surface. Growth in the prairie had practically ceased by June 22, 1933, following a period of three weeks of drought. The leaf surface actually decreased during the ensuing week, upon continuation of the drought, from 856 square inches per unit area to 823 (table VI). Upon resumption of growth, following ample rainfall, the leaf surface again increased, to 909 square inches during the following 15 days. The leaf surface also decreased in July, 1932, and later increased again after rains.

Corn made few demands upon the factors of its habitat and affected them but little until late in June. By this time, the prairie vegetation had been using much water, nutrients, etc., in an ever increasing ratio for at least ten weeks. Once the leaf area of corn decreased, as on August 14, it never again regained its maximum area.

The leaf area of prairie vegetation before June 1, was measured only during the season of 1933. An average square foot of little bluestem and its accompanying plant cover displayed at maturity 950, 1,050, and 1,014 square inches of leaf surface per unit area during 1931 and the two following summers, respectively. The maximum leaf surface of corn per square foot of soil surface during the same seasons was 437, 546, and 467 square inches or 46, 52, and 46 per cent as much, respectively (fig. 14). The thickness of the stand of corn for the three summers was not greatly different. In 1931, an average plant occupied 7.1 square feet; in 1932, 6.7 square feet; and in 1933, 7.3 square feet.

The prairie displayed approximately twice as much leaf surface at maturity, when it was 15 inches high, as did the mature corn which was about 90 inches tall. The leaf area in the cornfield decreased more after maturity

than did that of the prairie. This was due to the higher wind movement in the field which frayed and broke many of the leaves.

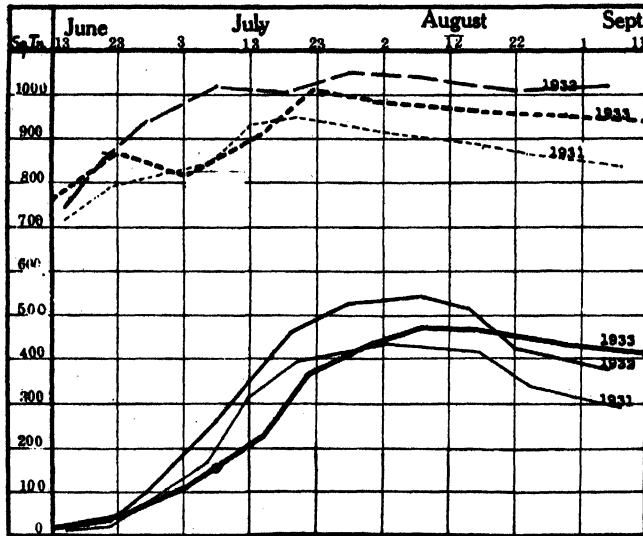


FIG. 14. Total leaf surface per square foot of soil in the two habitats during three years.

The denser cover in the prairie accounts for the lower light intensity, absence of air movement, higher humidity, lower temperature, and more uniform habitat at the soil surface in the prairie than in the cornfield.

WATER LOSSES AND PRODUCTION OF DRY MATTER

A battery of six phytometers was maintained at the prairie station throughout the three summers. It was prepared by transferring typical sods of *Andropogon scoparius* into cylindrical, galvanized iron containers one square foot in cross-sectional area and 16 inches deep. These sods were cut to fit exactly the containers and transferred into them without disturbance of the soil column or the root system within it. The containers were then placed in excavations of an exact size to receive them, with their tops even with the soil surface. In installing the phytometers extreme care was taken not to disturb the surrounding vegetation. A crop of grass matured in each container which was normal in every respect and indistinguishable from the surrounding vegetation (fig. 15).

Two other phytometers were similar to those shown in figure 15; in a fifth one the grass was killed, by adding hot water, and then removed. The soil thus bared was covered each week with the foliage cut from an area of the same size in the prairie. In a sixth phytometer the soil was kept denuded. The mulched and denuded phytometers, although operated singly, showed very consistent results.

The available water in the phytometers was maintained slightly above that

in the prairie during drought in order to support similar development of vegetation in the limited volume of soil. The height, thickness, and general development of the grass at any time, as well as the loss of weight of the



FIG. 15. Phytometers withdrawn from the soil showing little bluestem at the time of flower-stalk production on August 20, 1933.

phytometer, determined the amount of water to be added. They were weighed every 10 days and the water loss calculated in pounds per square foot of soil per day. Under extreme conditions the loss exceeded 2 pounds per unit area in a 24-hour period. Losses averaged 1.46 pounds per day for the three-year period; 1.21 pounds were lost from the denuded soil, and 0.86 pound from the mulched soil (fig. 16).

The water lost directly by transpiration is approximately the difference between the average daily loss from the normal phytometers and the mulched one, a daily average of 0.59 pound. Stated in terms of water transpired in relation to production of dry matter, it is 930 grams per gram of dry matter

produced. The loss of water by surface evaporation is approximately the difference between the average daily loss from the denuded phytometer and the mulched one, a daily average of 0.35 pound. The graphs in figure 16, representing the losses from the three types of phytometers, are very similar in trend except during hot, dry periods when losses from the grasses increase more than those from either the mulched or denuded surfaces.

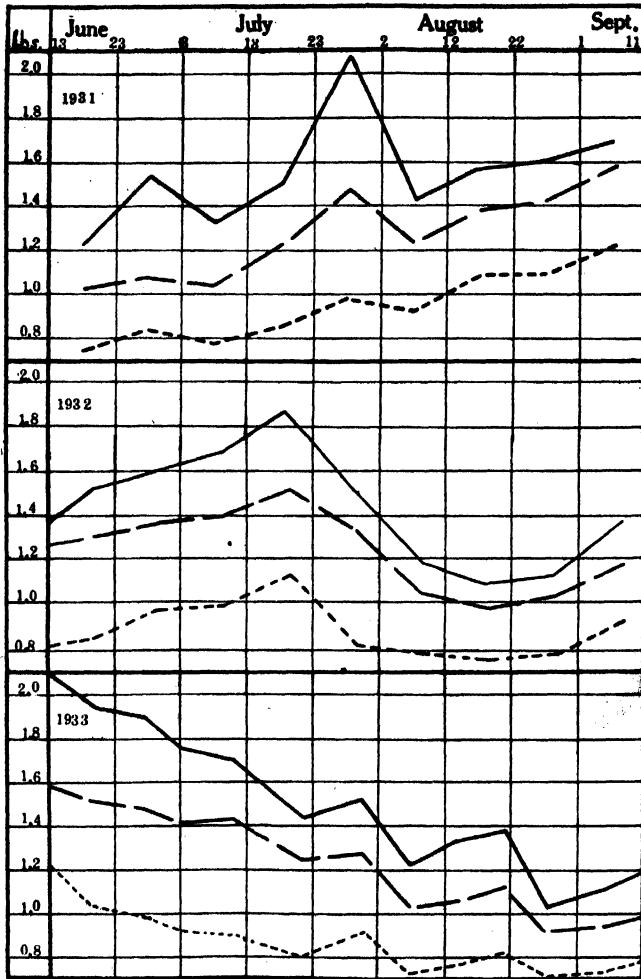


FIG. 16. Average daily water loss per square foot of prairie vegetation as measured by phytometers during three growing seasons. Solid line, from containers with vegetation; long-dash line, from bare soil; and short-dash line, from mulched soil.

The total loss of water per square foot in the prairie for the production of 1 gram of dry matter, during 1933, was 1,376 grams.¹ The total amount of water that might have been available to the prairie vegetation per square foot included the available water in the first 4 feet of soil at the beginning

¹ Complete data for the entire growing season of prairie, which begins about April 15, were taken only during 1933.

of the season and the water furnished by the precipitation on the area during the season, minus the available water in the 4 feet of soil at the end of the period of growth, assuming, as seems probable, that none moved downward beyond 4 feet. Since the volume weight of the soil at the several depths to 4 feet had been determined, the amounts of water present at the beginning and at the end of the season were readily calculated from the water content of the soil at these periods. At the end of the growing season, owing to good rains especially in July and early September, only one gram of this amount represented depletion of soil moisture in the upper four feet of soil. Subtracting the 1,154 grams used by the plants in transpiration, left a remainder of 222 grams which was lost by surface evaporation and run-off.

The corn phytometers were heavy galvanized iron cans 22 inches in diameter and 24 inches deep. Eight to ten such containers were used. Each held approximately 340 pounds of surface soil of about 15 per cent available water content. The lids were sealed in place with plasticene and adhesive tape with copious applications of shellac over all, insuring a waterproof seal (fig. 17). Plaster of Paris corks, 4 inches in diameter and 1 inch thick, were

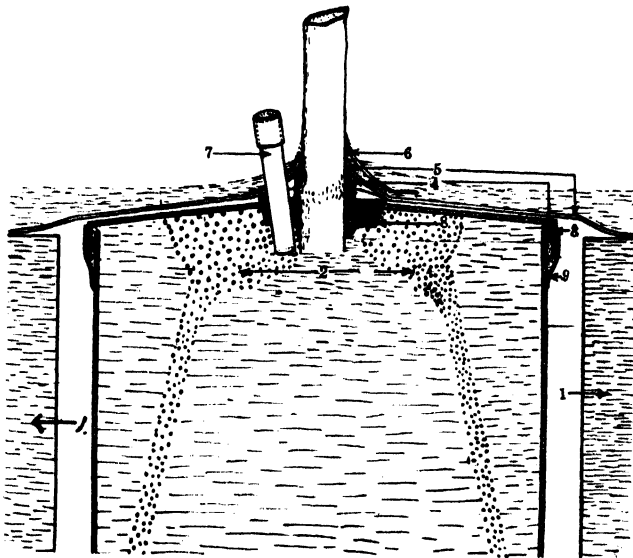


FIG. 17. Corn phytometer in trench showing seals, watering device and soil cover. 1, walls of trench; 2, catch basin filled with coarse sand; 3, cover of can; 4, plasticene seals; 5, oilcloth extending across can and trench; 6, oilcloth collar; 7, glass tube for watering; 8, plaster of Paris cork; 9, adhesive tape.

molded to fit the 4-inch opening in the center of the lids. A hole was made in the center of the cork for the cornstalk and another at the side for a tube to permit watering. The cork was made in halves so that it could be removed from time to time and the central hole enlarged to accommodate the growing corn. Water was prevented from running down the stalk into the phytometer by seals of plasticene and covers of oilcloth.

Penetration of moisture to all parts of the soil was insured by filling with coarse sand a depression in the center and top of each phytometer and also four wells, each an inch in diameter, extending to the bottom and outer portion of the soil. An oilcloth extended over the top of the phytometer and well over the sides of the trench. It was covered with 3 inches of loose soil. This type of installation insured normal soil temperatures and normal conditions of soil humidity as were determined by repeated measurements.

When the installation was completed, the casual observer could not distinguish the plants in the phytometers from those in the adjacent rows. A movable scaffold over the phytometers was equipped with a hoist to raise the phytometers to a large beam balance for weighing (fig. 18).

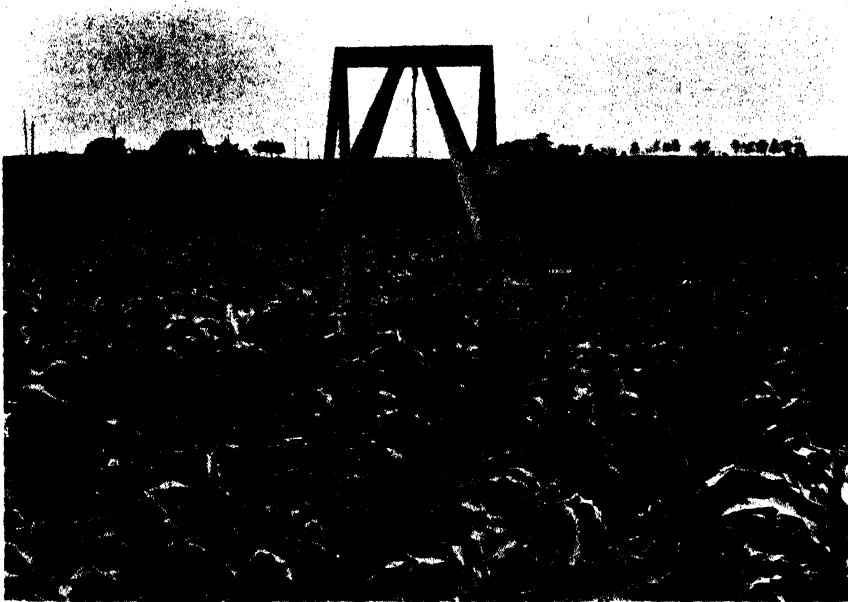


FIG. 18. Detail of station in cornfield, looking north. The phytometers extend from the camera case underneath the scaffold to the instrument shelters in the background.

The average daily transpiration loss, per square foot of soil surface, was .59 pound in the prairie, but 33 per cent less (.39 pound) in the cornfield. The average daily transpiration per square foot of soil was greater in the prairie than in the field throughout the entire summer of 1931. It was less in the prairie during a part of August, 1932, after a period of heavy precipitation, when the corn was tasseling. In 1933, transpiration in the field exceeded that in the prairie early in August and again at the end of August, following periods of heavy rains (fig. 19).

The water transpired during the dry summer of 1931 for each gram of dry matter produced was 406 grams. During the following summers the amounts of water transpired per gram of dry matter produced were only 274

and 271 grams, respectively. Calculations of the total amount of water lost both by transpiration and surface soil evaporation, made as were those for the prairie, showed that from June 1 to September 11, 1933, 786 grams of water

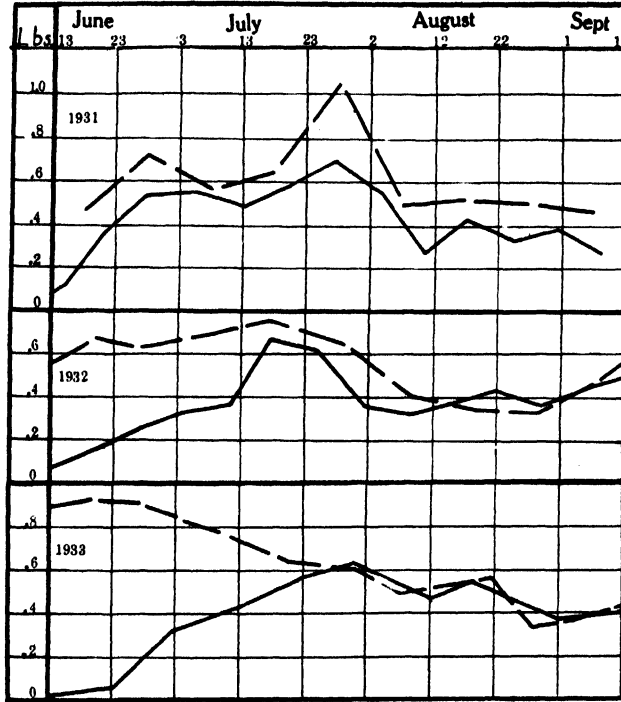


FIG. 19. Average daily transpiration, by weeks per square foot of soil, in the two habitats during 1931, 1932, and 1933. Solid lines, cornfield; broken lines, prairie.

were lost for each gram of dry matter produced. Of this total, only two grams represented the depletion of available moisture in the upper four feet of soil. The remainder, 513 grams, represented the amount of water lost by surface evaporation and run-off.

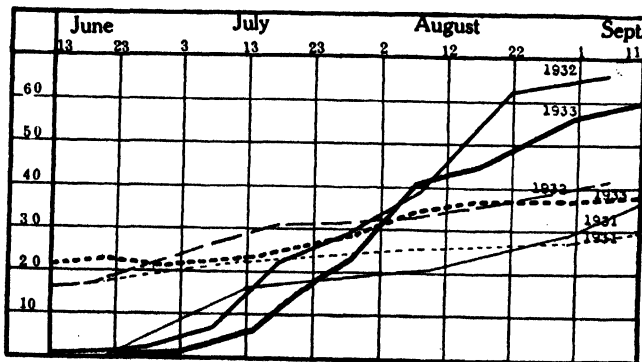


FIG. 20. Average production of dry matter in grams per square foot of soil in the two habitats during 1931, 1932, and 1933. Solid lines, cornfield; broken lines, prairie.

Corn was more efficient than prairie grasses in the utilization of water for the production of dry matter. This was due primarily to the longer growing season of the prairie grasses. After July 23, when both the corn and prairie grasses had nearly attained their maximum leaf surfaces the average daily transpiration losses were approximately the same, but the corn was producing much more dry matter per day (fig. 20). Hence during this period the corn was very much more efficient in the use of water than was the prairie.

The cornfield produced 35.9, 65.1, and 60.0 grams of dry matter, respectively, per square foot of soil in 1931, 1932, and 1933. The prairie produced 27.4, 40.3, and 38.1 grams. Thus the cornfield produced over 52 per cent more dry matter per unit of surface area of soil than did the prairie (fig. 20).

DISCUSSION

Weaver and Crist ('24) obtained an average daily loss of .85 pound of water per square foot of upland prairie vegetation during a period of 15 days (July 24–August 8, 1923). An average loss of 1 pound was obtained from the taller grasses on the lowland and 1.1 pounds from a square foot of soil surface in alfalfa. During the experiment the approximate sunshine was only 47 per cent, the average day humidity 80 per cent, and the average day temperature 79° F. The cloudy, humid weather readily accounts for a lower loss than that (1.4 pounds) determined in these studies.

The transpiration losses from corn in the production of dry matter are in close agreement with those of Kiesselbach ('16). He found average transpiration losses of 250 to 350 pounds for each pound of dry matter produced, the losses being higher in infertile soil.

In prairie vegetation, the plant cover or density of vegetation is adjusted to a normal water supply. Mature climax plants yield slowly to the effects of unusual conditions and are usually able to recover their normal state upon a return of normal conditions. Corn, on the contrary, quickly develops a large succulent top with broad thin leaves in response to an abundant early water supply stored up in the soil. Later it may be greatly harmed by extreme drought that may occur after the middle of July. It may be injured severely at such periods and never fully recover. Total leaf surface in prairie vegetation may decrease in response to drought only to again increase after the drought is broken. But when the leaf area of corn is reduced it never again increases.

No one climatological factor is responsible for development of vegetation. Each year a number of different combinations of factors may operate at different times. Transpiration losses are more responsive to environmental factors in each habitat until a good cover of vegetation is produced. After maturity of the leaves, changes are less marked.

Corn is more efficient in the production of dry matter from a given amount of water and soil area, but the destruction of native cover intensifies condi-

tions adverse to plant growth. It is entirely possible that the extreme periods of drought and hot winds of the midwest are in no small degree due to the destruction of the buffer effect of native climax vegetation. The increased production possible under cultivation is decreasing due to the destruction of organic matter, breaking down the soil structure, and erosion of the soil. A continuation of these processes under cultivation emphasizes the necessity of the reestablishment of some cover similar to the original climax vegetation. Natural equilibria must be increasingly relied upon in administration of natural resources (cf. Smith, '32; Weaver and Flory, '34).

SUMMARY

1. A comparison of physical factors, rate of transpiration, development of leaf area, and production of dry matter in climax prairie and a field of maize was made at Lincoln, Nebraska, during 1931 to 1933. The field had been broken and cropped to corn for three years previously.

2. Cultivation as practiced in the listed cornfield increased the volume weight of the soil, decreased porosity about 12 per cent, and retarded the rate of percolation 42 per cent or more. This resulted in greatly increased run-off and erosion compared to that in prairie.

3. There was a closer relationship between precipitation and available soil moisture at all depths in the native grassland than in the field.

4. Available moisture at all depths to 4 feet was usually greater in the field until the time of tasseling of the corn, about August 15. After this differences to the depth of two feet were not consistent and below two feet available soil moisture was nearly always greater in the prairie.

5. The percentage of dry matter produced each month in the prairie showed a close relationship to the percentage of the yearly precipitation occurring that month.

6. Mean day temperatures in the prairie averaged 3.9° F. lower and night temperatures 2.7° lower than those in the field.

7. During periods of very hot weather the average day temperatures were 7° F. less and the night temperatures 4° less in the prairie than in the field. The average daily temperature range in the prairie was 26° F., in the field 38° F.

8. Maximum temperature by weeks was sometimes 10° to 11° F. higher in the field and the mean maximum temperature for the three growing seasons was 4.8° F. higher.

9. The greater cover of vegetation in the prairie had a stabilizing effect which prevented the extremes of temperature that were found in the field.

10. The temperature of the air 4 inches above the soil surface in the prairie was higher than that of the soil at 3-inches depth; the reverse was true in the cornfield.

11. Average day humidity was 4.6 per cent higher in the prairie than in the cornfield, but average night humidity was only 0.3 per cent higher.

12. The differences between the average daily maximum and minimum humidities were 43.2 per cent in the field but only 34.5 per cent in the prairie.

13. When a maximum foliage cover had developed, light intensity at the soil surface in the field was 51 per cent, but in the prairie only 5 per cent; wind movement was 0.9 and 0.0 miles per hour, respectively. At mid-height of the vegetation light values were 65 per cent in the field and 24 per cent in the prairie; and wind movement 2.5 and 0.1 miles per hour, respectively.

14. Evaporation losses were always much less in the prairie unless the grass had been recently mowed.

15. Soil temperature at three inches depth averaged 8.2° F. lower in prairie, and at 8 inches depth 2.2° F. lower than in the field.

16. During the years 1931, 1932, and 1933, prairie vegetation displayed at maturity an area of 950, 1,050, and 1,014 square inches, respectively, of leaf surface per square foot of soil surface. The corn at maturity had developed 437, 546, and 467 square inches of leaf surface per square foot of soil surface.

17. The average daily loss of water per square foot of prairie was 1.46 pounds for the three-year period.

18. The average daily transpiration loss of plants per square foot of soil surface for the three-year period was .59 pound in prairie and 33 per cent less (.392 pound) in the cornfield. It was greater, however, in the field when the period of tasseling was accompanied by a high water content of soil.

19. The total amount of water used or lost in the production of one gram of dry matter in the prairie was 1,376 grams; about 32 per cent (445 grams) of this was lost in run-off and surface evaporation.

20. The total amount of water used or lost in the field for the production of one gram of dry matter was 786 grams; about 65 per cent of this was lost in run-off and evaporation from the soil surface.

21. Approximately 52 per cent more dry matter was produced per square foot of soil in the cornfield than in the prairie.

The writer wishes to acknowledge his indebtedness to Dr. J. E. Weaver for outlining the problem and for efficient direction throughout the course of the work. He is also indebted to Professor J. C. Russel for valuable suggestions concerning certain phases of the work on soils.

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CROWDING AND METAMORPHOSIS IN THE TADPOLE

W. GARDNER LYNN AND ABRAHAM EDELMAN

The Johns Hopkins University

It has long been known that the amount of space available to an organism during its life history and the degree of crowding to which it is subjected by other individuals of its own or other species may have profound effects upon its growth processes. The rate of growth as well as the ultimate size attained by the animal may depend to a considerable degree upon this so-called "space factor." The literature upon the subject of crowding and growth in animals generally is very well reviewed in Allee's ('31) "Animal Aggregations" and need not be taken up here. In the tadpole, detailed work on this subject has been done by Bilski ('21) and by Adolph ('31). The latter investigator, on the basis of periodic weight measurements of tadpoles raised in different volumes of waters, found ('31a) that although crowding has little effect upon the rate of growth during the first two weeks, the later growth rate is greatly affected, declining rapidly in crowded cultures. In addition to this effect however it was also found (Adolph, '31b) that those tadpoles which attained the greatest body size tended to undergo metamorphosis earlier than those which, under the influence of crowding, remained small. It is thus apparent that the time of metamorphosis of a group of tadpoles depends in some degree at least upon the number of individuals present in a given volume of water. This fact is of considerable importance in view of the wide use of the tadpole in laboratory studies of all kinds and especially those on endocrine secretions where the time at which metamorphosis occurs in different cultures is under investigation. Unless the space factor is controlled carefully it may easily cause serious inaccuracies in experiments of this type. An experiment similar to those of Adolph has recently been reported by Rugh ('34) in which an attempt at more accurate control of conditions was made. This study however was concerned only with the effect of crowding upon growth rate and the animals were not carried up to metamorphosis.

The experiment to be reported in the present paper was designed primarily as a further investigation of the correlation which may exist between available space and metamorphosis and observations of effects upon growth rate were recorded more or less incidentally. The species used was *Rana sylvatica*. Metamorphosis is, of course, an extremely complex phenomenon and care has been taken to control as many factors as possible. Fairly large numbers of animals have been used in order to avoid errors which may arise as a result of the great normal variations in viability and growth rate of tadpoles. Similarity in hereditary constitution was provided by using animals

from only two different egg masses. The eggs were allowed to hatch and the tadpoles were then thoroughly mixed before being counted out into the experimental chambers. It was decided that the problem of uniform feeding was best solved by having food available at all times for all animals and this was done throughout the experiment. The animals were fed rolled oats and occasionally the white of a boiled egg. To control conditions of temperature, light, oxygen tension and chemical constitution of the water an adaptation of the type of aquarium used by Rugh ('34) was employed. A large rectangular, glass aquarium measuring 320×590 mm. was divided into eight compartments of equal size by means of copper screening. The bottom of the screening was imbedded in sand and the ends were covered by split rubber tubing so as to fit tightly against the glass walls of the aquarium. The water level was kept at 70 mm. so that each compartment contained 1652 cc. of water. The temperature in such an aquarium remains very nearly uniform throughout. How rapidly the diffusion of gases and chemicals from one compartment to the others occurs is open to some question but it is believed that the chemical conditions in the different parts of the aquarium were fairly uniform. Certainly this arrangement gives much better control of these factors than could be obtained in cultures kept in separate dishes. The attainment of uniform conditions in all compartments was further aided by the way in which the tadpoles were distributed. This arrangement is shown in the diagram (fig. 1) from which it will be seen that compartments con-

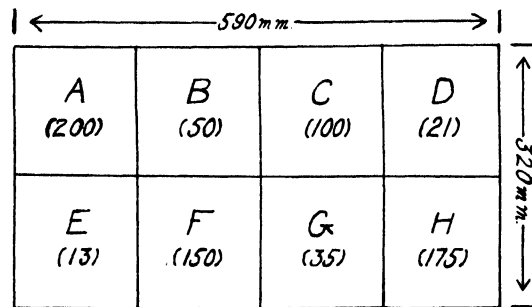


FIG. 1. Diagram of aquarium. The number of animals in each compartment is given in parentheses beneath the letter used to designate the compartment.

taining small numbers of animals were in proximity to ones having large numbers and vice versa. Food was changed and dead animals were removed daily. The water was changed but twice during the entire course of the experiment although some was added from time to time to replace that lost by evaporation.

The tadpoles were placed in the aquarium on March 20, two days after their emergence from the egg jelly. Daily observations were made and careful records of the time of appearance and growth of hind limbs and fore limbs were kept. The protrusion of the fore limbs was taken as a criterion

of metamorphosis and all records of the date of occurrence of metamorphosis refer to this feature. Once the fore limbs had appeared the animal was removed from the aquarium. All animals were measured on May 9. For this purpose calipers were used, the lengths being taken from the tip of the head to the tip of the tail. On May 27 the tadpoles in each compartment were weighed. Before weighing, the water was allowed to drip from the animals but they were not, of course, dry.

The results of the experiment are summarized in tables I and II. The

TABLE I. *Record of number of metamorphoses occurring in each compartment over the period May 8 to May 24*

Compartment	No. individuals	No. of individuals metamorphosing, May								
		8	10	12	14	16	18	20	22	24
E	13	1	2	1	1	3	2	1	1	
D	21	2	1		2		1	4		1
G	35		1			3	1	4	1	
B	50		1	2	1	6	4	5	3	
C	100					3	3	5	3	3
F	150					1		5	2	1
H	175					2		2	4	1
A	200		1	1		2	1	6	2	1

TABLE II. *Summary of the results of the experiment. The number of individuals in each compartment at the beginning of the experiment is given in the first column of figures, the number of completed metamorphoses in each compartment up to May 24 in the second column, and the number of individuals remaining at the end of the experiment in the third column. The percentage mortality and percentage of metamorphoses are recorded in the last two columns*

Compartment	No. individuals	No. metamor.	No. remaining	No. died	% mortality	% metamorphoses
E	13	12	1	0	0	92.3
D	21	11	10	0	0	52.4
G	35	10	25	0	0	35.0
B	50	22	23	5	10.0	44.0
C	100	17	42	41	41.0	17.0
F	150	9	84	57	38.0	6.0
H	175	9	57	109	62.3	5.1
A	200	14	58	128	64.0	7.0

first compartments to show metamorphosing individuals were the two containing the fewest individuals, compartments E and D. On May 8 one individual in E and two in D had free fore limbs. The last compartments to show metamorphosis were C, F and H in which individuals with fore limbs first appeared on May 16. Thus eight full days elapsed between the first appearance of metamorphosis in the crowded and uncrowded cultures. In other words the period of larval life of the most advanced tadpoles in the crowded cultures was extended about 15 per cent beyond that of the most advanced individuals in the uncrowded ones. It will be noted that com-

partment A, the one containing the greatest number of tadpoles, disagrees with the general result by showing a few metamorphosed individuals at a fairly early date, May 10. This may be at least partially explained by the fact that an exceptionally high death rate in this culture during the early weeks of the experiment brought the number of individuals down very greatly so that instead of containing the greatest number of individuals, this compartment was really in fourth or fifth place. The experiment was discontinued on May 24 at which time a number of tadpoles which had not yet undergone metamorphosis were still present in all compartments (table II).

The daily record of the number of metamorphoses occurring in each compartment is presented in table I. In order to save space the numbers are given for two day intervals. Table II gives a summary of the entire experiment giving the number of individuals present in each section at the beginning, the number of complete metamorphoses in each, the number of non-metamorphosed individuals present at the end of the experiment and the number which died during the period of the investigation. The percentage mortality and the percentage of successful metamorphoses in each compartment up to May 24 are given in the last two columns.

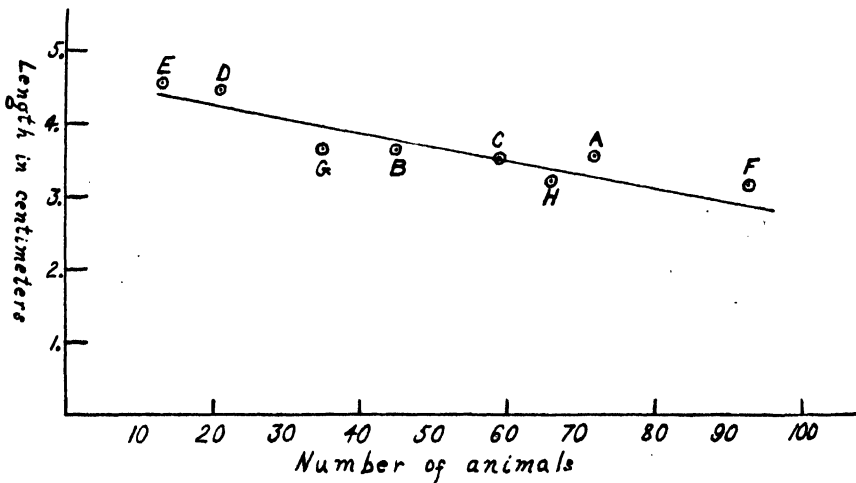


FIG. 2. Average body length in centimeters plotted against number of individuals present in the compartments at the time measurements were made, May 9.

The measurements of body length and of weight corroborate the findings of previous investigators and will be given only brief consideration. The animals having the most space available per individual were largest while those with the least available space were smallest and the individuals from compartments intermediate in this respect fell between the extremes in size. These relations are clearly shown on the two graphs (figs. 2 and 3). The lengths varied from an average of 455 mm. in the least crowded compartment to 314 mm. in the most crowded ones. The weights varied from .553 gms. per individual in compartment E to .249 gms. per individual in com-

partment F. The discrepancy shown in the results in compartment A due to the high death rate in the early part of the experiment is again evident here.

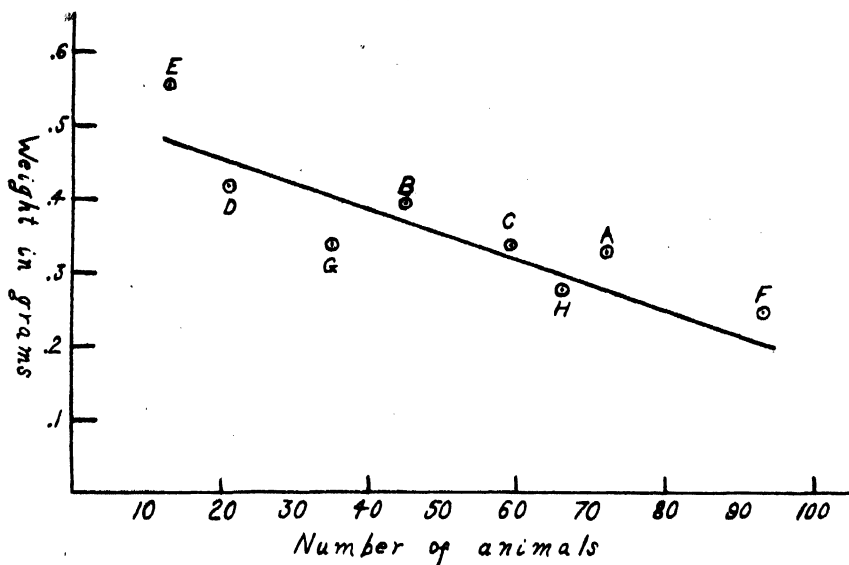


FIG. 3. Average weight in grams plotted against number of individuals present in the compartments at time of weighing, May 27.

CONCLUSIONS

The above experiment demonstrates two important effects upon metamorphosis which may be attributed to crowding. First, the retardation effect; the onset of metamorphosis is significantly delayed in the crowded cultures. Adolph ('31b) considers that this is a secondary result of the differences in body size of the individuals. Those in the least crowded cultures grow fastest and are able to metamorphose earliest. The animals in the crowded cultures grow more slowly and metamorphose later, not because they have then grown to the same size as the uncrowded tadpoles had reached at metamorphosis but because the deficiency in body weight has been compensated for by a surplus of age. This agrees well with our results; there is, as Adolph suggests, a complex set of factors at work and the effect upon metamorphosis can not be explained on the basis of the size differences alone.

A second effect of crowding upon metamorphosis is seen upon examining the last column in table II which shows the percentage of successful metamorphoses which had been undergone in the various compartments at the time when the experiment was discontinued. It seems very clear that the percentage of individuals which metamorphose successfully is very closely correlated with the space available per individual. The great difference in the percentages might have been considerably reduced if the experiment had been carried on for a longer period but could not have been entirely wiped out because of the fact that a high percentage of the animals in the crowded

cultures had already died without metamorphosing. Indeed, this effect may perhaps be ascribed entirely to the greater death rate in crowded cultures, a phenomenon which has frequently been noted.

Many ideas have been advanced to account for the effect of the space factor upon growth rate and body size and all of these must be given consideration in connection with the present work. Yung ('78,'85) attributed the decreased growth rate of tadpoles in crowded cultures to lack of aeration, and the work of Crabb ('29) on the snail tends to support this hypothesis. Adolph ('31a) however has clearly shown that while this may be an important factor it alone cannot account for the results. The accumulation of excretory products which have a harmful effect upon the organisms has often been suggested as the basis of the effect (Vernon, '95, Warren, '00, Crabb, '29, etc.), but again the results obtained in the experiments of Bilski ('21), Goetsch ('24), Adolph ('31a) and Rugh ('34) in which this factor has been controlled tends to show that this hypothesis is not an adequate one. Another factor which seems to be of much importance in the tadpole is the increased movement in the crowded cultures due to overstimulation of the animals as a result of frequent contacts. Bilski ('21) believes this to be the most important factor in the retardation of growth rate in crowded tadpole cultures. Adolph ('31a) has pointed out that tadpoles in crowded cultures do not feed so readily as do those in uncrowded ones, even though there is an excess of food available and suggests that this largely accounts for the reduced growth rate. It is probable that several of these factors are responsible for the results obtained in the present work, the effect of crowding upon metamorphosis being due to the action of these conditions upon bodily growth and upon the glandular complex which controls this phenomenon.

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RAINFALL RECORDS FOR THE SONORAN DESERT

T. D. MALLERY

Desert Laboratory, Tucson, Arizona

The scientific investigation of a region from the viewpoint of any branch of modern geography with its numerous ramifications should include accurate information concerning the climatic conditions. This is particularly true for biological studies in a typically arid region such as the Sonoran Desert of southwestern Arizona, southeastern California, and northwestern Sonora. Here the rainfall, because of its relative scarcity and uncertain distribution, is undoubtedly the most important climatic factor to be considered. It has a profound influence upon the survival and distribution of the various species which constitute the flora and fauna.

A record of the rainfall at the Desert Laboratory, Tucson, Arizona, has been kept since its establishment by the Carnegie Institution of Washington in 1903. The following year a raingauge was placed in the foothills of the Santa Catalina Mountains some ten miles distant from the Laboratory. Numerous other rainfall stations were established from time to time and were maintained for longer or shorter periods in connection with experimental projects. In 1925, however, an extensive investigation of the rainfall on the Sonoran desert area was begun.

The pronounced local nature of the majority of the storms in this region made it essential that as extensive an area as practical be included in the study. Two principal lines of raingauges were established along diverging routes from Tucson and a series of gauges has been concentrated on the grounds of the Laboratory and in the immediate vicinity. The approximate location of most of these rainfall stations is shown by Sykes ('31) on a map of southern Arizona and northern Sonora. Since his publication appeared additional stations have been established. Figure 1 shows the location of the stations for which data are presented in this paper.

The series of gauges known as the Libertad line extends in a southwesterly direction from Tucson to Cirio Point, formerly designated as Kino Point, nine miles south of Puerto Libertad, Sonora, on the Gulf of California. The outstanding features of the topography and of the vegetation along the Libertad line have been presented by Shreve ('24). Each gauge has been located at a point which possesses some particular botanic or topographic feature.

The Camino line of gauges follows a route which leaves the Libertad line 24 miles west of Tucson. This route continues on to Ajo, 135 miles west

from Tucson, thence south to the international boundary and then in a west-northwest direction along the old Camino del Diablo emigrant trail. An interesting history of this route together with nine photographic views taken at various points and personal experiences while travelling it have been published

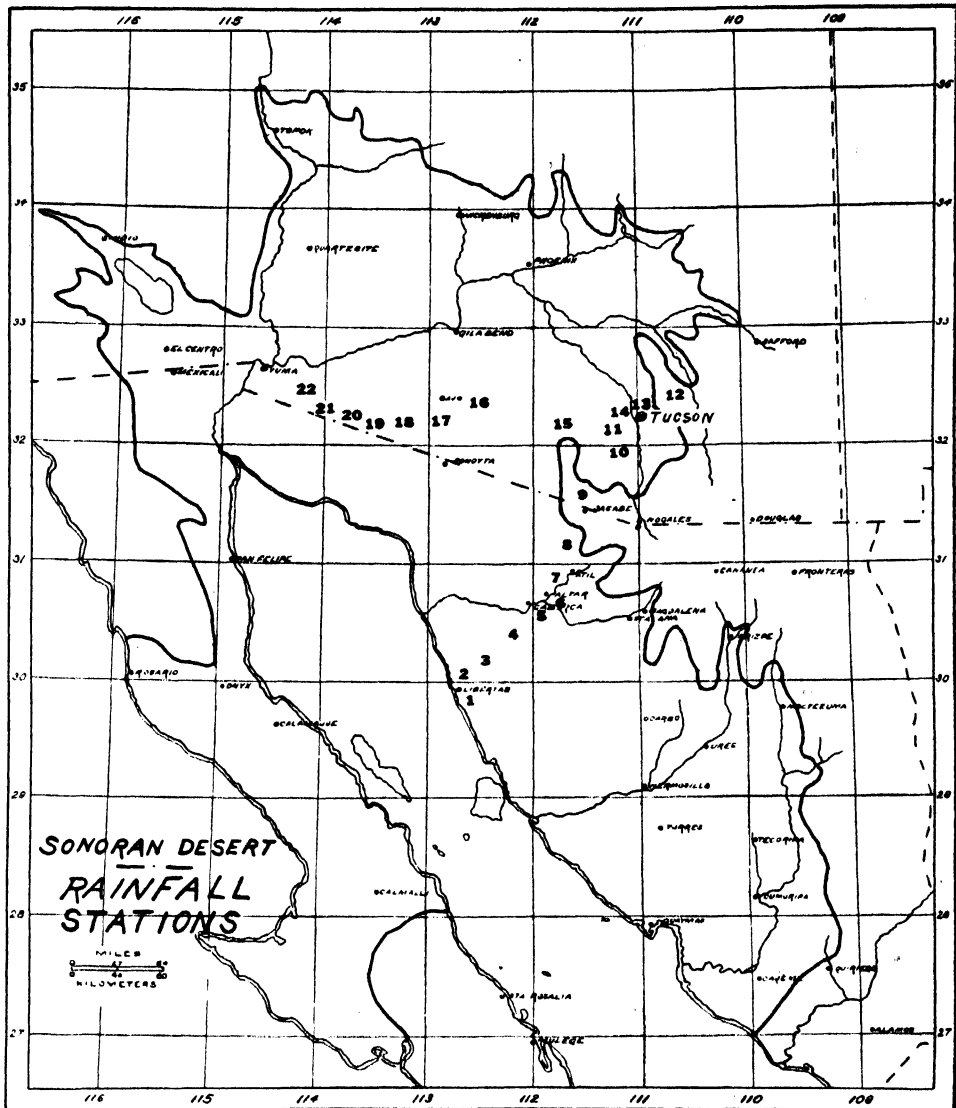


FIG. 1. Map showing the location of the long-period raingauge stations and their relation to the Sonoran Desert area which is shown delimited by the heavy boundary line.

by Sykes ('27). The furthest raingauge is 10 miles south of Wellton, Arizona, and approximately 40 miles southwest of Yuma, Arizona. The most distant gauges on the Libertad and the Camino lines are each approximately 245 miles by road from Tucson and 180 miles by airline.

The distribution of the rainfall in the region under consideration is usually concentrated in two distinct seasons of the year. These are the winter rainy season and the period of summer rains. As Sykes ('31) points out the approximate normal expectancy is that 35 per cent of the total annual precipitation will fall during December, January, February and March and 45 per cent during July, August, and September. Because of this fact and also because it is often quite impossible to visit the gauges at the end of the calendar year, due to the condition of the roads, the plan was adopted of reading the gauges each spring and fall, or, more specifically, during the months of April and October unless prevented by unusual weather conditions or other uncontrollable circumstance. Considerable freedom has been exercised in choosing the exact dates for the readings since the primary interest has centered in the comparative amounts of winter and summer rainfall.

In carrying out such a program it is obvious that a type of rain gauge must be used which will prevent evaporation of the rainwater between readings. To fill this need Godfrey Sykes has developed a long-period gauge¹ which is proving very satisfactory. A quantity of dynamo or motor oil (100 cc.) prevents the evaporation of the rainwater between readings. This gauge is described rather thoroughly in the paper by Sykes ('31). Figure 2 shows the long-period gauge in various stages of use. Until recently the funnel of the gauge was made of sheet copper, as is the receptacle. Now the funnels are turned from brass and contribute to a much more rigid and durable piece of equipment. Some readings have been lost because the copper funnel was damaged by cattle, wild animals, and displaced rocks. It is believed that the brass funnels will reduce this type of accident.

Sheet copper has proved very satisfactory for making the receptacle of the gauge because it can be subjected to considerable stretching and bending without breaking. None of the Sykes' gauges has burst even when exposed to freezing temperatures at high elevations throughout the winter. An interlocking type of seam is used in the construction. Another advantage of the copper is, of course, that it does not rust.

The extensive use of this type of gauge has taught the author several things which are related here as suggestions for those who may desire to carry on similar investigations with long-period gauges. The most satisfactory vessel to use in measuring the rainfall collected in a gauge is a one-litre graduated glass cylinder. The glass permits one to determine when the separation of oil and water is complete and the ten cubic centimeter divisions permit readings which are sufficiently accurate for all practical purposes. After emptying a gauge it is a good practice to rinse it out thoroughly with kerosene before replacing it. This removes any accumulation of surplus oil, insects, lizards, dust, etc., and keeps the gauge in good working order. It has also

¹ This type of rain gauge may be obtained from the Fred C. Henson Scientific Instrument Co., 3628 E. Colorado St., Pasadena, Calif. The price subject to change, is \$7.50 each or \$60 per dozen.

been found advisable to label the gauges stating what they are and to whom they belong. Since the gauges are usually buried up to the necks in soil or rocks the most effective place for the identification label is on the funnel, although a supplementary legend on the receptacle is also advisable. The peculiar shape and neat appearance of a gauge makes it quite attractive to



FIG. 2. The long-period Sykes' raingauge; 1, gauge with funnel detached; 2, field carrying case showing 100 cc. graduate cylinder filled with oil for resetting gauge, two one-gallon cans for oil and kerosene, a quantity of cotton waste, and the one-liter graduate containing the rainwater and oil (note line of demarcation) just poured from the gauge on the right; 3, gauge in place on the ground with only the funnel and a portion of the spout exposed.

souvenir hunters and more especially so if they cannot identify their find. When a number of gauges are to be serviced in the field it is well to construct a box in which a one litre graduate, a 100 cc. graduate, a quantity of oil, a quantity of cotton waste or rags, and one gallon of kerosene may be conveniently carried to the respective stations. Such a box conserves much energy and greatly reduces the graduated cylinder mortality. A trowel, a geologist's hammer, and a shovel are also useful additions to the field equipment.

The total capacity of the gauge is approximately 4,500 cc. This is equivalent to nearly 39 inches of rainfall and is sufficient to accommodate

yearly readings in most situations and readings at high elevations on the basis of the semi-annual inspections. Since the diameter of the funnel is three inches, 115.878 cc. is equivalent to one inch of precipitation. For the degree of accuracy possible with this apparatus the use of the conversion factor 116 is acceptable.

The effectiveness of the oil seal in preventing evaporation of the rain-water between readings has been tested many times. The most recent test was begun on April 6 and terminated on Dec. 16, 1934. Two gauges were placed side-by-side on the flat black roof of a stone building. One-hundred cc. of oil were placed in one gauge and 1,000 cc. of water in the other. During the period of exposure the gauge containing the oil received an increase in its liquid contents equivalent to 6.46 in. of rainfall. This quantity was equal to 0.52 in. more than the amount of precipitation retained by the gauge which contained no oil.

To test further the reliability of the Sykes' long-period gauge, one was placed beside a Standard Weather Bureau for two periods of one year each. The weather bureau gauge was read immediately after each storm while the long-period gauge was read only at the end of each year. The first year the standard gauge was read 51 times for a total of 10.57 in. of rainfall. The long-period gauge contained 10.71 for that year or 0.14 in. more than the standard gauge. During the year 15 traces of rain were recorded for the standard gauge. It is quite probable that the accumulation of these traces in the Sykes' gauge would account for the difference between the totals. The second year the standard gauge was read 62 times and caught 9.30 in. while at the end of the year the Sykes' gauge yielded 10.13 in. Here again the 12 traces of rain recorded during the year might have amounted to a sufficient accumulation to account for a greater part of the difference. Slight errors in reading the standard gauge could easily make up the remainder of the difference.

STATIONS

LIBERTAD SERIES

1. Cirio Point, formerly erroneously called Kino Point, is a low range of granitic hills which project into the Gulf of California about 9 miles south of Puerto Libertad. It is so named because of the presence of the Cirio (candle) tree, *Idria columnaris*, the most conspicuous plant on a very restricted area at this place. These are the only known representatives of this species of the family Fouquieriaceae outside of the desert region of Lower California. The gauge is approximately one half mile from the beach at an elevation of about 180 feet. The most characteristic plants in the immediate vicinity of this station are *Olneya tesota*, *Jatropha cinerea*, *Simmondsia californica*, *Idria columnaris*, *Ptiloria pauciflora*, *Hibiscus denudatus*, *Elaphrium rhoifolium*, *Fouquieria splendens*, *Encelia farinosa*, *Trixis angustifolia*, *Verbesina chihauhuensis*, *Franseria dumosa*, *Opuntia bigelovii*, and *Hyptis emoryi*.

2. Puerto Libertad is a small fishing village on the Bay of Libertad which is guarded on the north by Lobos Point and on the south by Cirio Point. The distance between these protective arms is about 12 miles. The gauge is approximately one-half mile from the bay and 100 feet above sea level. The vegetation is very sparse. *Fouquieria splendens*, *Larrea tridentata*, *Olneya tesota*, and *Prosopis glandulosa* are the most abundant. A few scattered representatives of *Pachycereus pringlei*, *Ferocactus lecontei* and *Opuntia gosseliniana* are also present.

3. Nineteen miles east from the Gulf the road passes over the Picu Mountains at an elevation of 1,620 feet. The summit of this pass is in the midst of a veritable botanic garden which is distinguished by a great variety of small trees, shrubs, and shrub-like perennials. The most common species of these are *Prosopis velutina*, *Cercidium torreyanum*, *Parkinsonia microphylla*, *Elaphrium microphyllum*, *Olneya tesota*, *Jatropha spathulata*, *Larrea tridentata*, *Encelia farinosa*, *Horsfordia alata*, *Abutilon sonorae*, *Euphorbia tomentulosa*, *Franseria dumosa*, *Simmondsia californica*, *Acalypha adenostachya*, *Abutilon palmeri* and *Franseria deltoidea*.

4. Fifty-Mile Pass is a low pass through a group of volcanic hills 50 miles by road from Puerto Libertad. The elevation of this station is nearly 1,400 feet. The vegetation at this location is composed principally of *Parkinsonia microphylla*, *Elaphrium microphyllum*, *Carnegiea gigantea*, *Olneya tesota*, *Opuntia fulgida*, *Larrea tridentata*, *Fouquieria splendens*, *Acacia constricta* and quantities of the grass, *Hilaria mutica*.

5. Las TempORAles station is on the north slope of an isolated volcanic hill at an elevation of 1,100 feet. It is approximately 10 miles south of the town of Pitiquito. The perennial plant species here are *Lemaireocereus thurberi*, *Parkinsonia microphylla*, *Olneya tesota*, *Carnegiea gigantea*, *Opuntia spinosior*, *Ferocactus wislizeni*, *Prosopis velutina* and *Larrea tridentata*.

6. This gauge is on the roof of Hacienda de Oquitoa, 6 miles east of Altar, Sonora, on the Altar River. The elevation here is 1,700 feet. The vegetation in the immediate vicinity is determined and influenced largely by agricultural practice using irrigation. The native vegetation on the surrounding hills however is typically desert and includes such species as *Larrea tridentata*, *Opuntia fulgida*, *Carnegiea gigantea*, *Prosopis velutina*, *Fouquieria splendens* and *Parkinsonia microphylla*.

7. Red Rock Crossing, so named because of the brick red color of the sandstone formation exposed in the bed of the wash, is 9 miles north of Altar, Sonora. A gauge was placed here because this location is the northern limit of the distribution of *Lemaireocereus thurberi* or organ pipe cactus, on this route. The elevation is 1,700 feet. *Fouquieria splendens*, *Carnegiea gigantea*, and *Parkinsonia microphylla* are common in this region.

8. This rainfall station was established a short distance south of Rancho Los Molinos because *Lophocereus schottii*, the senita cactus, is seen at this point for the last time as one travels north. The plant association is prac-

tically the same as at station number 7. This gauge is 2,340 feet above sea level.

9. The Baboquivari station is 2.8 miles north of San Fernando, Arizona, and 3.3 miles north of the international boundary. The elevation here is 3,675 feet, the highest station in this series. The vegetation is principally range grasses interspersed with scattered patches and individual plants of *Prosopis velutina*.

LOCAL SERIES

10. At the Sierrita Mountains station the gauge is on a gently sloping north exposure at an elevation of 4,100 feet. This is an open grassland region with scattered *Prosopis velutina*, *Opuntia* sp. and other cacti.

11. The Avra Valley gauge is on the floor of the valley directly north from the Sierrita Mountain station toward the Tucson Mountains. Its elevation is 2,400 feet. There are dense growths of *Prosopis velutina* in the neighborhood of this station. *Acacia gregii*, *Acacia constricta*, *Carnegiea gigantea*, and *Opuntia fulgida* are also common.

12. This station is located at Soldier Camp on the main ridge of the Santa Catalina Mountains, which border the Tucson area on the northeast. The elevation at this place is 7,875 feet and while it is excluded from the desert by reason of this altitude it is included in this series for the purpose of comparing the rainfall of the higher elevations with those of the desert. A distinctly mesic type of vegetation covers these mountains at elevations above 7,000 feet. Several species of conifers are present including *Pinus arizonica*, *P. strobiformis*, *P. chihuahuana*, *Pseudotsuga taxifolia*, *Juniperus pachyphloea*, and *Abies concolor*. *Quercus emoryi*, *Q. hypoleuca*, and *Q. gambelii* represent the oaks and *Alnus acuminata*, *Acer interior*, and *Arbutus arizonica* are also found. Snow is an annual occurrence at this station and therefore the precipitation records are probably lower than the actual total, since the gauge is not designated to measure snowfall. Care was exercised in locating the gauge on a ridge where the snow does not drift.

13. The Pima Canyon gauge is located at the Desert School near the entrance to the canyon on the south slope of the Santa Catalina Mountains directly north across the Santa Cruz Valley from the Desert Laboratory and at approximately the same elevation as the Laboratory, or 2,600 feet. The most abundant species in the vicinity are *Parkinsonia microphylla*, *Prosopis velutina*, *Fouquieria splendens*, *Carnegiea gigantea*, *Jatropha cardyophylla*, *Encelia farinosa*, and *Opuntia* sp.

14. Nine long-period rainfall stations are located on the grounds of the Desert Laboratory, an area of approximately 850 acres. Tumomoc Hill rises to an elevation of 2,950 feet on the northeast quarter of the grounds and the remainder of the area, called the campus, is relatively level at approximately 2,400 ft. One gauge is located on the summit of Tumomoc Hill and one at the approximate center of the "Campus." The remaining four stations are

around the border of the grounds and near the extremities. The purpose of this concentration of stations is to determine the variations in precipitation within relatively short distances. The perennial vegetative cover of the grounds is quite homogeneous, varying somewhat in density with elevation and soil changes. The most prominent species are *Larrea tridentata*, *Parkinsonia microphylla*, *Prosopis velutina*, *Opuntia* spp., *Carnegiea gigantea*, *Encelia farinosa*, *Franseria deltoidea*, and *Fouquieria splendens*.

CAMINO DEL DIABLO SERIES

15. Sells, Arizona is 65 miles west of Tucson and is 2,500 feet above sea level or 100 feet higher than Tucson. It is in a region of low rolling hills and low mountain ridges. The dominant plant species present are *Larrea tridentata*, *Prosopis velutina*, *Fouquieria splendens*, *Parkinsonia microphylla*, *Aplopappus hartwegi*, certain grasses and *Olneya tesota*.

16. Twenty-three Mile Hill is a small, isolated volcanic hill 23 miles east of Ajo, Arizona. The gauge is on the north slope of this hill at an elevation of 2,350 feet. The outstanding plants found here are *Carnegiea gigantea*, *Opuntia spinsior*, *Opuntia fulgida*, *Fouquieria splendens*, *Encelia farinosa*, *Franseria deltoidea*, and *Parkinsonia microphylla*.

17. The Growler Pass station is on the gentle southwest slope of the Growler Mountains about 21 miles south of Ajo. The elevation is 2,250 feet. *Larrea tridentata* is quite common here in the ground covering of small dark brown shiny stones known as desert pavement. *Olneya tesota*, *Prosopis velutina*, and *Carnegiea gigantea* have a scattered representation on the plain while *Parkinsonia microphylla*, *Lemaireocereus thurberi*, *Fouquieria splendens*, and *Opuntia fulgida* occur on the hills nearby.

18. From Growler Pass a plain on which *Larrea* is the dominant plant is crossed toward the southwest for a distance of 12 miles to Agua Dulce where a gauge is located near some low hills. Mountains by the same name are only a few miles distant to the south. *Olneya* and *Prosopis* occur in the low spots and washes, *Larrea* is dominant on the plain along with *Franseria deltoidea*. Scattered plants of *Carnegiea gigantea* are present. The vegetation on the hills is very sparse. *Elaphrium microphyllum* is seen for the first time on the slopes. The elevation is about 1,140 feet.

19. The lava flow from the Pinacate Mountains of Sonora is crossed on this route 22 miles west of Agua Dulce at a point where the plateau is about 3 miles wide. The volcanic plateau is approximately 910 feet above sea level here and it extends northward about 6 miles. Bryan ('25) characterizes this mesa as rising "from 50 to 100 feet above the Tule Desert, and this elevation seems to measure the thickness of the olivine basalt of which it is composed. Small cones and craters dot the surface. Volcanic bombs are numerous."

20. The Tule Tank station is 18 miles west of the Pinacate Plateau on the south slope of a low granitic mountain of the type so characteristic of

southwestern Arizona. The exposed rounded granitic surfaces support very little vegetation. *Larrea*, *Fouquieria*, *Parkinsonia*, *Prosopis*, *Encelia*, and *Olneya* are common on the gently sloping plains between the ranges. A more mesic type of vegetation grows in the small drainage channel immediately below the natural waterhole or tank at the base of a small canyon nearby. The elevation of this station is about 1,115 feet.

21. A series of nine natural waterholes or tanks, holding several hundred gallons each when full, located in a vertical series on the north slope of the mountain range is responsible for the name Tinajas Altas, or High Tanks, which is used for these mountains and for this rain gauge location. The rock formation and vegetation is similar to that at Tule Tank which is 20 miles distant. *Larrea*, *Encelia*, *Parkinsonia*, *Olneya* and *Carnegiea* are found on the mesa at the base of the mountains. The elevation is about 1,050 feet.

22. The most distant gauge in this series is located in the Lechuguilla Desert 10 miles northwest of Tinajas Altas and 12 miles south of Wellton, Arizona. The desert floor in this vicinity slopes very gently northward so that the drainage does not follow deep cut channels but spreads out over the entire plain. Channel-cutting is becoming more evident each year, however, due principally to the removal of vegetation by cactus collectors and wood cutters. *Larrea*, *Carnegiea*, *Franseria*, *Encelia*, *Prosopis*, and *Olneya* are the most common species. *Echinocactus polycephalus* and several species of *Opuntia* also occur in this region. The elevation is approximately 715 feet.

PRESENTATION AND DISCUSSION OF THE DATA

In tables I and II a summary of the rainfall data obtained to date is given for the various stations. The numbers preceding the names of the stations correspond to the numbers used in the descriptions of the stations and their locations on the map. The figures in parentheses following the readings indicate the number of readings upon which the averages are based. In many cases the number of annual readings and of summer and winter readings do not agree. This is due to the fact that sometimes no reading was obtained because the gauge had been disturbed or removed and also in some years it was not possible to make semi-annual trips to the stations.

It is unfortunate that the stations were not all established at the same time so that direct comparisons could be made between stations with greater confidence. From the data presented, however, certain observations concerning the rainfall pattern of this region may be made. In general as the elevation increases the rainfall increases. This is brought out more clearly by selecting for comparison only those stations for which four or more annual totals are available. Dividing these stations into four groups according to elevation we find that those below 1,000 feet have an annual average of 4.19 inches; those between 1,000 and 2,000 feet, 8.10 inches; those between 2,000 and 3,000 feet, 11.03 inches; and those stations above 3,000 feet, an annual average of over 25 inches of rainfall.

TABLE I. Long-period raingauge readings for the Libertad Series and the Local Series to May 1934. The figures in parentheses indicate the number of readings upon which the average is based

Station	Elev. in ft.	Date estab.	Average Precipitation		
			Summer	Winter	Annual
<i>Libertad Series</i>					
1. Cirio Point.....	180	April '25	2.66 (8)	1.42 (7)	4.03 (9)
2. Puerto Libertad.....	100	April '25	2.44 (8)	1.57 (7)	4.82 (8)
3. 19 Mi. Pass.....	1,620	April '25	8.51 (7)	2.45 (7)	10.96 (7)
4. 50 Mi. Pass.....	1,400	April '25	10.06 (9)	1.76 (8)	12.08 (9)
5. Las Temporales.....	1,100	April '31	5.94 (3)	0.93 (2)	10.87 (3)
6. Oquitoa.....	1,700	Oct. '32	5.68 (2)	2.13 (2)	7.82 (2)
7. Red Rock Crossing.....	1,700	April '32	10.32 (3)	2.30 (2)	14.57 (2)
8. Los Molinos.....	2,340	April '32	7.62 (2)	3.80 (1)	11.38 (1)
9. Baboquivari.....	3,675	April '31	12.33 (3)	4.41 (2)	16.33 (3)
<i>Local Series</i>					
10. Sierrita Mts.....	4,100	May '28	10.90 (6)	4.49 (5)	16.66 (6)
11. Avra Valley.....	2,400	Nov. '26	5.58 (6)	2.96 (4)	10.25 (4)
12. Soldier Camp.....	7,875	May '26	18.38 (9)	15.37 (6)	33.42 (6)
13. Pima Canyon.....	2,600	May '30	8.07 (4)	3.33 (3)	10.27 (4)
14. Desert Laboratory Grounds.....	2,400				
A. Near N. Gate.....		April '26	7.99 (8)	3.43 (6)	11.71 (6)
B. Midway between N. & S. Boundary.....		May '28	6.22 (5)	4.11 (4)	12.55 (6)
C. N.W. Corner.....		June '30	5.40 (4)	4.20 (3)	13.06 (4)
D. S.W. ".....		June '30	5.37 (4)	3.81 (3)	12.22 (4)
E. S. of Tumamoc Hill.....		June '30	5.75 (4)	3.89 (3)	13.21 (4)
F. Summit of Tumamoc Hill....	2,950	Nov. '26	7.54 (7)	3.67 (7)	10.83 (8)

TABLE II. Long-period raingauge readings for the Camino Del Diablo Series to December 1934. The figures in parentheses indicate the number of readings upon which the average is based

Station	Elev. in ft.	Date estab.	Average Precipitation		
			Summer	Winter	Annual
<i>Camino del Diablo Series</i>					
15. Sells.....	2,500	Mar. '32	5.53 (2)	3.41 (2)	8.94 (2)
16. 23 Mile Hill.....	2,350	Jan. '29	7.24 (3)	3.75 (2)	11.24 (5)
17. Growler Pass.....	2,250	Mar. '32	3.88 (3)	4.14 (2)	8.56 (2)
18. Agua Dulce.....	1,140	Oct. '26	4.04 (5)	3.63 (5)	8.19 (8)
19. Pinacate Plateau.....	910	May '28	2.44 (4)	2.25 (3)	3.72 (6)
20. Tule Tank.....	1,115	June '26	2.25 (6)	1.42 (5)	3.71 (7)
21. Tinajas Altas.....	1,050	June '26	2.01 (6)	2.64 (5)	5.56 (7)
22. Lechuguilla Desert.....	715	Oct. '32	1.38 (2)	2.47 (2)	3.86 (2)

Aside from elevation another factor, namely, the distance from the Gulf of California, seems to influence the amount of rainfall. Although stations 20 and 21 are above 1,000 feet they have annual averages of less than 6 inches. In fact, stations 19 to 22, which are relatively near the Gulf, all have averages which are quite close to those for stations 1 and 2, which are on the Gulf. This indicates that moisture arising from the Gulf of California is carried a

considerable distance inland before it is precipitated and that the mountains of Southwestern Arizona are too low and hot to initiate condensation. It is also quite possible that the western end of the Camino del Diablo Series is out of the path of clouds from the Gulf, when the prevailing direction of the wind is from the west and northwest.

The average annual records found for stations 9, 10, 14, 16, and 17 agree quite closely with those published by Smith ('30) for stations which are relatively near to these or are in similar situations. Table III indicates these similarities.

TABLE III. *Comparison of rainfall data from standard U. S. Weather Bureau gauges by Smith and data from Sykes' long-period gauges at nearly or similar stations*

From data by Smith			From Tables I and II above		
Station	Elev.	Annual Rainfall	Station	Elev.	Annual Rainfall
Baboquivari	4,000	17.24 (6)	9. Baboquivari	3,675	16.33 (3)
Helvetia	4,000	18.34 (12)	10. Sierrita Mts.	4,100	16.66 (6)
Tucson	2,387	10.96 (12)	14. A-E Desert Lab.	2,400	12.55 (4-6)
U. of Ariz. Tucson	2,423	11.51 (53)	14. Summit of Tumamoc	2,950	10.83 (8)
Ajo	1,770	9.88 (14)	17. Growler Pass	2,250	8.56 (2)

An intensive study of desert rainfall on the grounds of the Desert Laboratory by Humphrey ('33) showed that the mean annual rainfall as recorded in 24 gauges 100 meters apart on a 300 meter square tract with an ascending lateral extension of 800 meters was different in almost every gauge. The author points out, however, that there was a flattening of the individual differences between gauges during the year and that the mean annual readings would no doubt continue to become more equal if the records were obtained for a period of years. This will also be true for long-period gauge records for similar but more widely separated areas since the fluctuations due to the spotted distribution of the summer thunder storms in particular will tend to become equalized and only the permanent factors such as altitude, distance from the loci of storms, prevailing winds, and topography will remain effective. At several of the stations gauges have been set out within a short distance of each other. Readings from such duplicates have always agreed remarkably well except when one of the gauges had been disturbed or a difference in the size of the funnel of some of the older gauges was found by careful measurement.

While a knowledge of the total annual rainfall at any given place serves as a fundamental starting point for the scientific treatment of the climate of that region it does not give the distribution of the individual storms. The distribution is more important from the standpoint of the vegetation and of erosion than is the total yearly amount. Shreve ('34) emphasizes the fact that the irregularity of the rainfall in desert regions greatly increases the adverse char-

acter of the conditions for plants and that there is little relation between annual rainfall totals and the amount of moisture in the soil. Data are presented which show conclusively the importance of the duration of a storm, the relative dryness of the ground surface at the moment the rain starts, and the weather conditions immediately following the rain in determining the amount of penetration and runoff. Rains of less than 0.15 in. were found to be ineffective in increasing the soil moisture at 15 cm. unless they fall on soil which is moist and are followed by cloudy weather. Runoff does not usually accompany rains of less than 0.75 in.

A satisfactory long-period recording raingauge has not yet been invented. Therefore, it is not possible to get accurate distribution data for the rainfall of out-of-the-way places such as are included in the series of raingauge stations reported on in this paper. The biennial readings are more informative than annual readings alone would be and the use of averages, when based upon sufficient readings, gives a more accurate indication of the amount of rainfall to which the plants and animals must become adjusted. Drought escaping plants probably profit by unusually wet years or seasons. It is doubtful, however, whether the true desert xerophytes are greatly aided in growth by precipitation above the average or are severely injured during subnormal years. Reproduction of some desert plant species may be benefitted by wet seasons during which the soil moisture is maintained sufficiently high to permit the seedlings to become established. The continuation of such conditions over a period of months, however, would be fatal for many species. It is planned to continue the long-period rainfall study of the Sonoran Desert for another period of years in order to make the average readings still more valuable as indicators of the desert environment.

The writer is greatly indebted to Dr. Forrest Shreve, in charge of the Desert Laboratory, for his helpful criticisms and suggestions during the preparation of this report.

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CLIMOGRAPHIC STUDIES OF CERTAIN INTRODUCED AND MIGRATORY BIRDS¹

ARTHUR C. TWOMEY

University of Illinois

Considering the relation of animals to their environments, one may conclude that where natural factors limit the range or distribution of a species, usually very few complicated factors are involved. The extent to which these factors actually limit in their effect ordinarily involves not the entire life-cycle of the species or the individual, but some particular or critical period of the life of the organism. Of all the periods in this life cycle, the breeding season followed by that in which the young are raised, is undoubtedly the most critical. At such periods the environmental conditions must be as nearly optimum as possible else catastrophe results. By optimum is meant that which is most suited to the physiological requirements of the individual. The tolerance of the adult is greater than that of the young, and if the conditions under which the young are raised are too far from this optimum, the young will perish though the adult may survive, but such a sequence of events quickly results in the extermination of the race.

It is not the purpose to review here the many studies of physiological conditions and physical factors which control the movements of an organism. Many studies have been made involving temperature, humidity, rainfall, and radiation, as *individual* factors influencing or limiting the distribution of animals, but there are few studies which take into consideration a possible combination of two or more of these factors as indicating the range preference or range limitations of a species. The author has been unable to find any work using two factors as a means of measuring or comparing certain phases of the migration problem of animals, or to explain either the obvious success or equally obvious failure of species introduced into a new environment.

The purpose of this study is to present two distinct problems of avian life history by means of duplex data involving both temperature and humidity. These two problems are: (1) the problem of the introduced species: why it is either a success or a failure; and (2) a comparison of the summer and winter ranges of certain migratory birds as shown in terms of these two factors, temperature and humidity. The first involves the question: Can we, in terms of temperature and humidity, show any cause or reason why certain species have been introduced successfully into certain regions and entirely unsuccessfully into others? The second involves the questions:

¹ Contribution from the Zoological Laboratory of the University of Illinois No. 473.

Is there any relation, in terms of temperature and humidity, between the summer and winter ranges of certain species of birds? Do they migrate from one set of physical conditions into a region characterized by a different or by a similar set of conditions? Can the answer to these two questions throw any light on the problem of migration routes or destinations?

In order to analyze the conditions under which different birds are living, climographs have been employed, which show the temperature-humidity conditions within the range of the species involved. These climographs, made for the optimum conditions of the species studied, are used as the basis for comparison of the conditions into which the introduced species are projected or into which the migratory species move.

Climographs have been used by ecologists for a number of years to show that a combination of the two factors, temperature and rainfall, play an important part in nature. Both are definitely controlling factors on the environment in general and may be considered as vital to the organisms within that environment. Climographs serve as a basis of comparison for temperature and humidity in various localities (Shelford, '30).

THE PROBLEM OF THE INTRODUCED SPECIES

Since the coming of settlers into North America, many attempts have been made to introduce various species of birds into America, both from Europe and from the Orient. There have been some outstanding failures. The English Sparrow and European Starling are among the notable but unfortunate successes; each bird has been able to adapt itself to varied and extreme conditions. This is proven by the fact that the English Sparrow has had such a wide range over North America, the Hawaiian Islands, Bermuda, Cuba, South America, Australia and New Zealand and by the fact that the Starling is certainly doing exceedingly well in its new North American environment. It appears that the birds do very well anywhere outside the tropics but do not fare so well beyond latitude 50 degrees. Other imported birds, as the Hungarian Partridge, for example, have been outstanding successes in certain definite localities, though failures in others. This shows that the bird has a limited range tolerance and cannot exist under such a wide range of the limiting factors of temperature and precipitation as can a bird like the English Sparrow. The European Sky Lark is another notable example because of its very local successes in the United States. The Chinese Starling brings out a further example of a bird that has spread but locally. It apparently cannot stand cold temperatures and has remained on the Pacific coast, moving gradually southward as far as Portland, Oregon. Many more examples could be cited, but all seem to show that imported birds will perish unless they obtain an optimum both of temperature and precipitation highly similar to those existing in their native habitat at least during the critical time of nesting.

The following examples show how climographs which consider only temperature and rainfall throw light on the reasons for some imported birds being successful in their new environment, for others being complete failures, and still others showing partial or local success.

The Hungarian Partridge (*Perdix perdix perdix*) is a good example of the last type, an importation locally successful. It is a bird which has a wide range in its habitat preference. Introduced from central Europe a few years

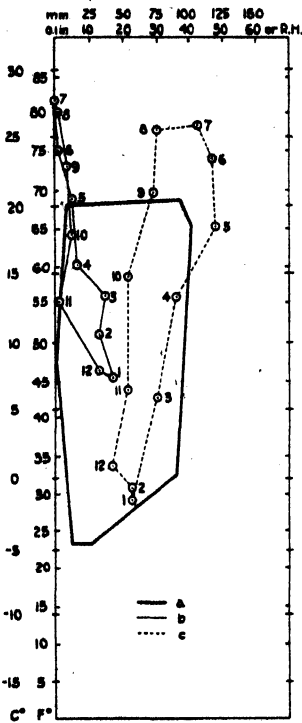


Fig. 1

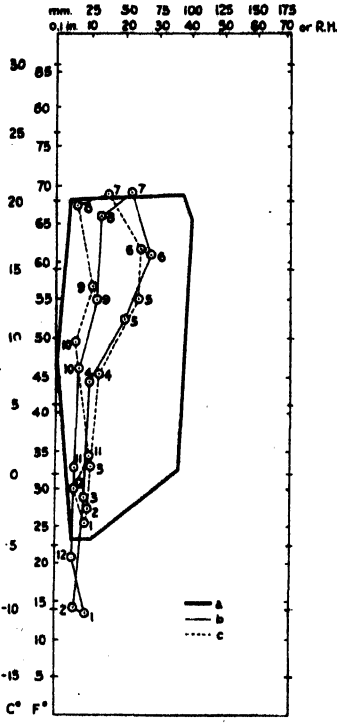


Fig. 2

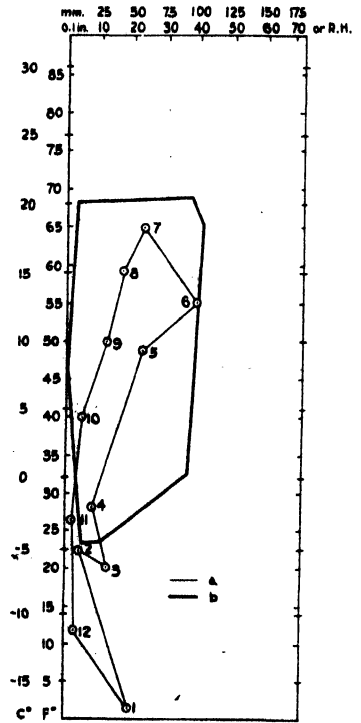


Fig. 3

Climographs for Hungarian Partridge

- FIG. 1. (a) European optimum
(b) Frenso, California
(c) Columbia, Missouri.
- FIG. 2. (a) European optimum
(b) Havre, Montana
(c) Great Falls, Montana.
- FIG. 3. (a) Edmonton, Alberta
(b) European optimum.

ago, it has been distributed by extensive plantings throughout the United States and Canada. It has flourished exceedingly well in some states, while in others, it has failed completely. In California, Missouri, and New Jersey, the Partridge has failed to establish itself despite the state wide planting operations. Available data show that these states have all that is required for the physical comfort of the bird, and food is not scarce. The yearly

optimum for the temperature of each state is nearly identical with that of central Europe. There is also a close correlation in respect to yearly mean rainfall. But when, by means of the climograph, the optimum conditions of temperature and rainfall for each month had been established for the range of the Partridge in central Europe, and this compared with the climographs of these areas of failure (fig. 1), very little correlation is in evidence. Studying the climograph (fig. 1), one sees clearly that in both cases the months that fall outside the optimum conditions are 5, 6, 7, 8, and 9 (May to September),

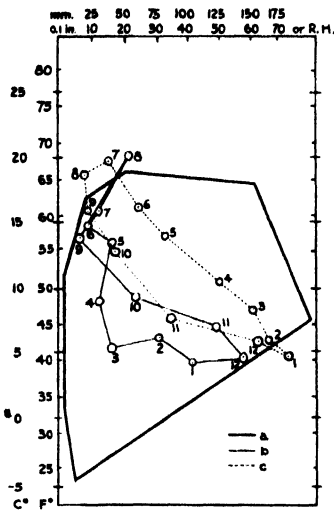


Fig. 4

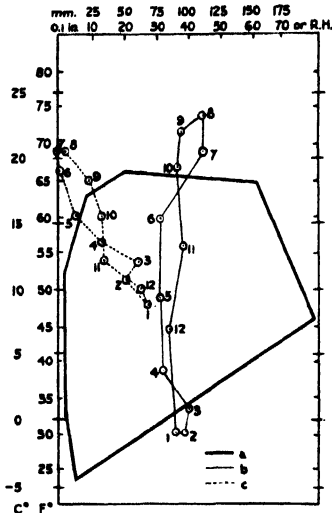


Fig. 5

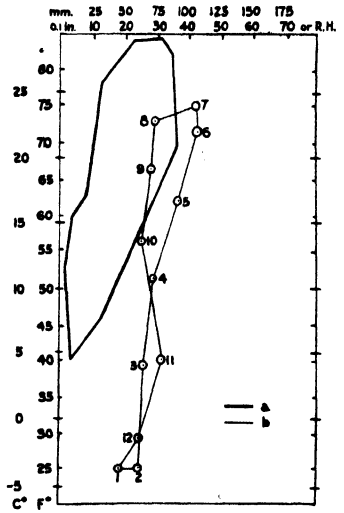


Fig. 6

Climographs for European Skylark

- FIG. 4. (a) European optimum
(b) Victoria, British Columbia
(c) Portland, Oregon.

- FIG. 5. (a) European optimum
(b) Brooklyn, New York
(c) San Jose, California.

Climograph for Texas Bob-white

- FIG. 6. (a) Native optimum in Texas and Mexico
(b) Urbana, Illinois.

the critical periods in the life cycle of these birds. It is during these months that the eggs are laid and the young are hatched and reared. California is too hot and dry during the nesting period; Missouri and New Jersey experience too much rain and high temperatures during this critical period.

On the other hand, in south and central Alberta (fig. 3) where the Hungarian Partridge has flourished and has spread over a very wide area within a brief span of about fifteen years, the climograph falls within the optimum conditions of its native habitat in central Europe. Months 1, 2, 3, and 12 fall

considerably below the optimum, but low temperatures during this time of the year do not, apparently, affect the birds. However, it is clearly seen that the critical months 5, 6, 7, 8, and 9 all fall very well within the optimum conditions.

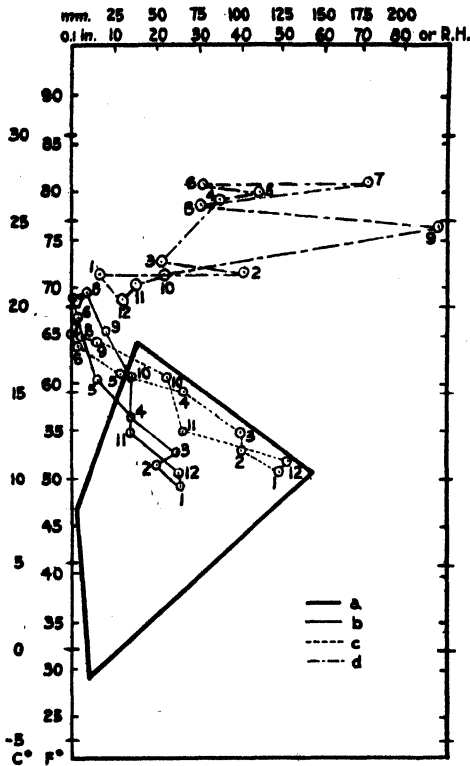


Fig. 7

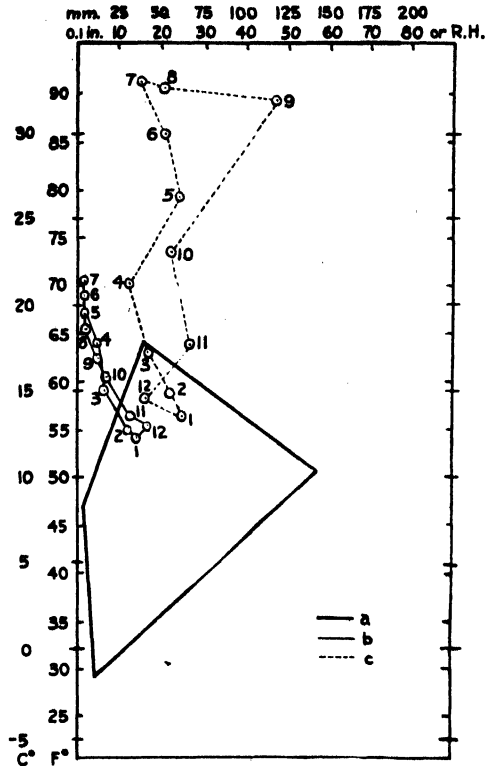


Fig. 8

Climographs for Long-Billed Dowitcher

- FIG. 7. (a) Breeding optimum in Alaska
(b) San Jose, California
(c) Santa Cruz, California
(d) Havana, Cuba.

- FIG. 8. (a) Breeding optimum in Alaska
(b) San Diego, California
(c) Corpus Christi, Texas.

The birds have likewise been successful in parts of Montana where state wide plantings were carried on. The north central portions of the state have the largest successful populations as indicated by the climograph (fig. 2). Great Falls lies inside the optimum for all months, though Havre has months 1, 2, and 12 falling outside. Here again is evidence that in localities where the birds are successful, the critical months of 5, 6, 7, 8, and 9 are all inside the native optimum conditions.

A similar example can be cited in the case of the Texas Bob-white (*Co-*

linus virginianus texanus) which was thought capable of flourishing successfully in Illinois. Extensive plantings were made around Urbana and numerous other areas in the state, but all were total failures. Figure 6 brings out one very probable reason for the failure. The optimum conditions of temperature and rainfall in Urbana are almost entirely outside of the optimum conditions for its native habitat in Texas and New Mexico. One would prophesy in advance by reference to such a chart, that the planting of this bird was pre-doomed to failure.

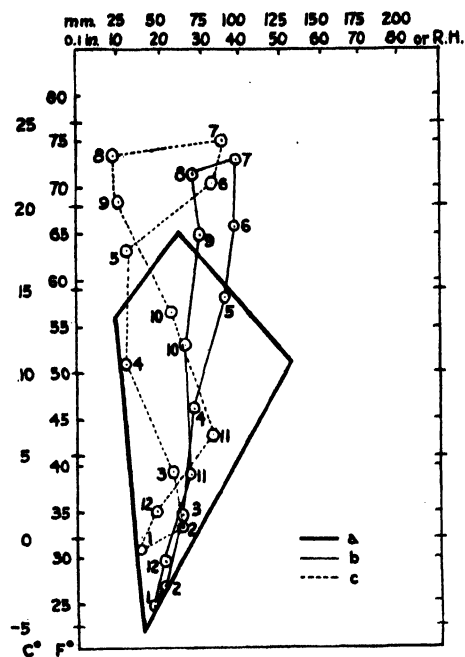


Fig. 9

Climograph for Bohemian Waxwing

- FIG. 9. (a) Breeding optimum for Edmonton, Alberta; Ungava, Quebec; and Moose Factory, Ontario
 (b) Chicago, Illinois
 (c) Pittsburgh, Pennsylvania.

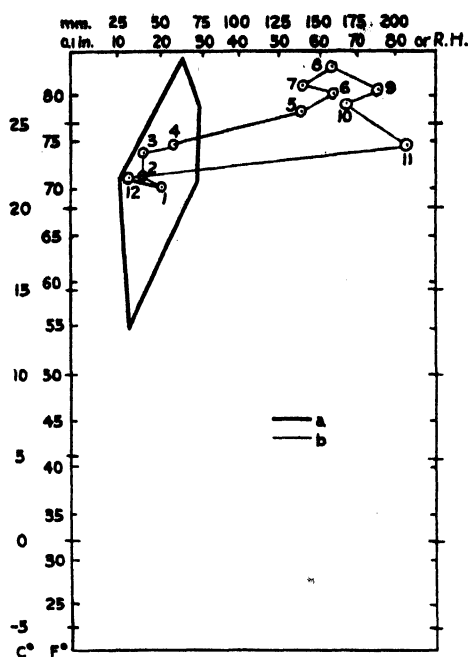


Fig. 10

Climograph for Kirtland's Warbler

- FIG. 10. (a) Breeding optimum—counties of Oscoda, Crawford, and Roscommon, Michigan
 (b) Bahama Islands.

The European Skylark (*Alauda arvensis*) is a common bird in England and central Europe. The optimum distribution in England and Germany shows a considerable range for this bird (fig. 5). It was introduced into Brooklyn, New York about 1870 where it flourished for twenty years. Many accounts of it were published in "The Auk" during this time, but it

had disappeared by 1899. A severe blizzard in February, 1888 was supposed to have caused its doom.

From the above account, it appears that they were fairly successful in Brooklyn. On glancing at figure-5, it may be seen that the optimum ranges of temperature and rainfall for Brooklyn fall precariously within the Skylark's native optimum conditions. It is important, however, to stress the fact that the critical breeding and nesting months of 5 and 6 fall within the native optimum conditions though the subsequent semi-critical months fall just outside. In Portland, Oregon where it was introduced in 1889, the Skylark spread locally and flourished for twenty to twenty five years. The climograph (fig. 4) shows that the greater part of the year falls within the Skylark's optimum range, especially for the months of 5 and 6, and no critical months fall far outside. That 7 and 8 fall outside would indicate a precarious situation, however.

From all data available it seems evident that the Skylark is a success in the neighborhood of Victoria, B. C., where it was planted in April, 1913. Fifteen years later it was still present near Victoria and frequently has been heard singing. A glance at the climograph (fig. 4) shows clearly that the optimum temperature and rainfall for all the critical months of the year fall within the native optimum; only August is slightly outside. Similar plantings were made near San Jose, California in 1896 (fig. 5). It was reported that they were doing well the following year, but that they finally vanished. The optimum range for San Jose shows that the critical months of 5, 6, 7, 8, and 9 are all considerably outside the bird's native optimum and one would not expect its survival.

THE PROBLEM OF THE SUMMER AND WINTER RANGE

The second problem involves a comparison of the summer and winter range of certain migratory species of birds. Possible causative agents of migration are not considered in this paper. The fact of migration—that certain birds leave a definitely circumscribed area of summer activities, and after a long journey, winter in another circumscribed area—is considered here. A comparison of this summer and winter area in terms of temperature and humidity has been made in an effort to ascertain whether there is any relation between them in terms of these two climatic factors. Birds having a "definitely circumscribed" summer and winter range have been chosen merely because such birds indicate a relatively limited climatic tolerance, and hence are much more easily studied than wide-ranging, highly tolerant species. Finally, the choice of species has been limited because of the small number of weather stations in the extreme north and in the area of winter distribution, from which data could be obtained to construct the climograph of the area. The following examples show two things: the climatic relationship of the summer breeding and the inter ranges, in terms of temperature and humidity, and the fact that "strays" from the normal range, driven perhaps by storm

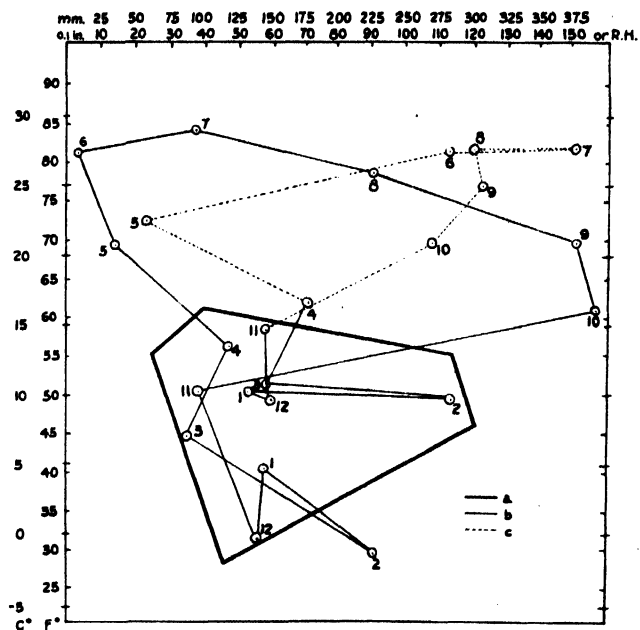


Fig. 11

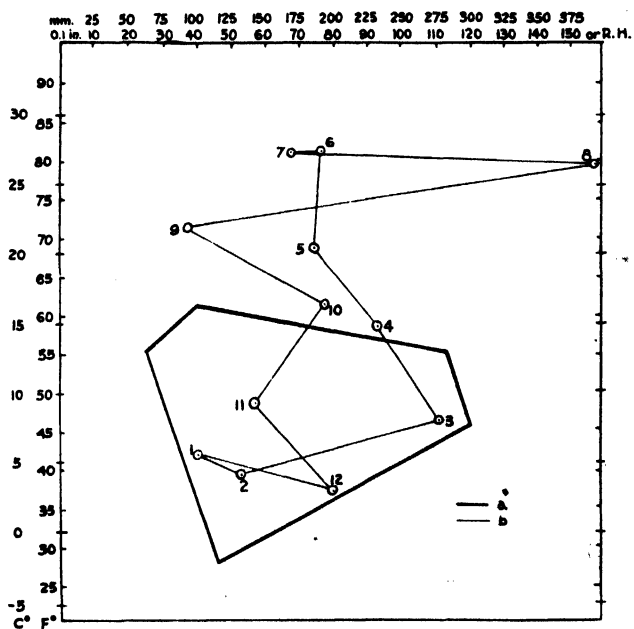


Fig. 12

Climographs for Tree Sparrow

- FIG. 11. (a) Breeding optimum—Churchill, Manitoba; Moose Factory, Ontario; Ungava, Quebec
 (b) St. Louis, Missouri
 (c) Charleston, Illinois.

- FIG. 12. (a) Breeding optimum—Churchill, Manitoba; Ungava, Quebec; Moose Factory, Ontario
 (b) Nashville, Tennessee

or other event from the normal migration route of the species, are actually far out of their optimum.

The Long-billed Dowitcher (*Limnodromus griseus scalopaceus*) arrives on its breeding grounds in northern, north central and north western Alaska late in May. The nesting occurs during June, and by the middle of August the young are fully grown and ready for the fall migration. The optimum conditions for these months, 5, 6, 7, 8, and 9 for this Alaskan area have been used in plotting the optimum summer conditions, with the results shown in figures 7 and 8 by the area involved in the heavy black figure. From this optimum breeding area the birds migrate down the California coast, and are common winter residents along this coast from San Diego to southern California. Within this range three points were selected: San Diego, San Jose, and Santa Cruz, California. The mean monthly temperatures and humidities for these three localities are plotted in figures 7 and 8. It is interesting to note that the months 10, 11, 12, 1, 2, 3, and 4 all fall within the optimum summer range of the species in all three locations. In other words, the winter conditions of the temperature and humidity factors in San Diego, Santa Cruz, and in San Jose, California, are within the range of those same conditions in northern Alaska in the summer, and that the Longbilled Dowitcher, in migrating from Alaska to San Diego, San Jose, or Santa Cruz for the winter, has simply exchanged one set of conditions for the same set of conditions in another locality. The Dowitcher is also found in winter at Corpus Christi, Texas. By plotting the climograph for this location in winter, it is found that the winter months 12, 1, 2, and 3 fall within the range of the Alaskan summer conditions. At Havana, Cuba, the Long-billed Dowitcher is a rare straggler, and Havana is outside the normal winter range of the species. The climograph of Havana (fig. 7) shows clearly that one would not expect the Dowitcher there at any time of the year except by accident, for not a single month touches the summer conditions in the Alaskan breeding area.

The Bohemian Waxwing (*Bombycilla garrula pallidiceps*) is a bird whose wanderings are extensive. It nests regularly from western Alaska across northern Canada to northeastern Manitoba. Plotting the climograph for the summer range within this extensive breeding area, widely separate stations were selected—Edmonton, Ungava, and Moose Factory. These give the form represented by the heavy black outlined area of figure 9 when the breeding months of the Bohemian Waxwing are plotted. This species winters near Chicago, Illinois, and around Pittsburgh, Pennsylvania. Figure 9 shows that in the climograph of Chicago and Pittsburgh the months of 5, 6, 7, 8, and 9 all lie outside the breeding range of this bird, while the rest of the year, including those months spent by the bird outside of its summer range, all fall within the climograph of the two cities. Here again the bird has exchanged its summer range for a winter range involving the same set of conditions.

Kirtland's Warbler (*Dendroica kirtlandi*) has perhaps the most restricted breeding range of any of our song birds, for it is known to breed in only three counties of the state of Michigan—Oscoda, Crawford, and Roscommon. The winter range is restricted to the Bahamas and at least as far south as the Caicos Islands. The climograph of the Bahamas winter range is shown in figure 10. In this same figure the summer breeding range is indicated by the heavy outlined area. It is interesting here to note that the months of 12, 1, 2, 3, and 4 of the Bahamas winter range fall inside of conditions within the optimum breeding area during the breeding season.

Finally, the Tree Sparrow (*Spizella arborea arborea*) offers an excellent example. The breeding range of this bird is the Hudson Bay area of Canada. Its southern limit extends into the central and south central United States. The heavy black line in figures 11 and 12 represent the summer breeding optimum which comprises the same set of conditions found at Churchill, Manitoba, Moose Factory, Ontario, and Ungava, Quebec. The climograph illustrated by figure 11 shows that for Charleston, Illinois, the months 11, 12, 1, 2, and 3 fall within the breeding optimum. Likewise, the months 11, 12, 1, 3, and 4 are within the optimum for St. Louis, Missouri. A further example (fig. 12) shows that the months of 11, 12, 1, 2, and 3 for Nashville, Tennessee, are all within the summer optimum. Thus this bird also tends to choose the same set of conditions for its winter range as that of its breeding optimum.

I wish to acknowledge my indebtedness to Dr. A. R. Cahn of the Department of Zoology of the University of Illinois, under whose guidance the work was done.

SUMMARY

1. Bird species of limited distribution live within a limited set of environmental factors which form the optimum conditions for that species.

2. If that species be introduced into a new locality, in which the environmental conditions during the critical period of the year are too diverse from the native optimum, the species will not be able to maintain itself, and will disappear. In localities where the local optimum lies partially within the native optimum, the species may linger in a precarious state, or may be eliminated at any time by serious local disturbances in the climatic factors.

3. Birds which live under a wide range of tolerance tend to establish themselves quickly and to spread rapidly over their new environment.

4. Climographs may be used to show whether or not an introduced species will thrive successfully in a given locality.

5. Barring other factors of the environment such as food and shelter, a species introduced into a new locality is destined to failure unless the optimum conditions of temperature and humidity coincide with those conditions in the native habitat, at least during the critical season of the breeding period.

6. The main reason for failure of introduced birds is that the critical

nesting period falls outside of the optimum conditions in the native habitat.

7. Extremes of temperature and rainfall do not necessarily affect introduced birds after the critical period has passed.

8. Migratory birds with a restricted summer range, tend to seek the summer optimum of temperature and rainfall in their winter range.

9. Migratory birds with a wide climatic tolerance of both nesting and winter ranges are not strongly affected by the two factors of temperature and rainfall.

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CERTAIN SOCIOLOGICAL ASPECTS ASSOCIATED WITH PLANT COMPETITION BETWEEN NATIVE AND FOREIGN SPECIES IN A SALINE AREA

VERNON A. YOUNG

New York State College of Forestry, Syracuse, New York

Plant sociology has exercised a strong influence on the science of ecology and workers are constantly on the alert for new problems which may throw additional light on the subject. A desirable field which offers such an opportunity is the study of the sociological relationships of the foreign and native species to each other in America. Among the many inviting and favorable geographic regions in the United States for such a study, New York State is quite outstanding because of the nature of its topography and soils. The soils ranging from the saline seashores to the extremely acid bogs of the Adirondack Mountains are quite heterogeneous in their physical and chemical composition and offer in certain localities desirable habitats for the growth of foreign plant invaders. This condition together with the ease with which foreign plants entered the state through foreign shipments before quarantine laws were enacted now reveals cosmopolitan plant communities well stabilized in both natural and cultural habitats. In addition to these, denuded areas are constantly occurring by the excavation of large areas for road building materials, waterways and manufactured products as well as associated fills and residue dumps. These new physiographic areas where the soils are raw and sometimes rich in certain residue salts are highly desirable for the study of certain sociological relationships of native and foreign plants as to successional behavior under unusual environmental conditions.

A new physiographic area located along the southwest shore of Onondaga Lake at the terminus of the old Erie Canal, which borders the City of Syracuse, N. Y., is similar to a condition mentioned above and forms the nucleus of the present investigation. This area, approximately one-quarter of a mile wide and one mile long, is a saline residue dump or fill about 12 feet high, deposited 34 years ago by a chemical manufacturing company. The soil is a finely ground limestone which was chemically treated and is therefore rich in salts, the principal ones being calcium carbonate, calcium chloride, sodium carbonate, sodium chloride, and potassium sulfate. Salt incrustations still occur in a few small areas slightly lower than the general surface. With the exception of a few embankments used for the pipe line which discharged the residue, the general upland region is comparatively level. Along the lake shore footslopes, terraces and ravines are evident where the soil is better drained than the main upland area of the fill.

A preliminary investigation of the region revealed the heterogeneity of the soil and showed that the vegetation consists of a highly cosmopolitan community of foreign and native species. Various ecological problems are suggested. The specific purpose in the present paper is twofold: to draw attention to the aggressiveness of certain foreign and native species to establish a plant community where many other species are unable to reach ecesis because of the adverse environmental conditions, and to furnish evidence that a certain degree of sociological adjustment is introduced with competition among such species in a community from the initial pioneer stage to and including the edaphic climax which is highly correlated with the physical and chemical changes of the soil.

RESULTS OF QUADRAT STUDIES OF THE UPLAND VEGETATION

Quadrat studies showed the vegetation is not typical of New York, but a highly cosmopolitan community composed of 29 herbaceous species, and 12 grasses, and according to table I, 18 of the former and 6 of the latter are of foreign origin. The vegetation as a whole represents several species well adapted to habitats of unusual edaphic conditions. It was also evident that the vegetation of the main area which is sparsely distributed is not as far advanced in the succession as the dense vegetation of the foot-slopes and ravines facing the lake frontage. Therefore, the physiographic and climatic features of the region, although not extreme, may have determined to a high degree the species which became the original pioneers as well as the rate of successional change.

Linaria, *Sporobolus*, and *Salsola* Stage

The data obtained from the quadrat studies¹ definitely indicate that *Linaria minor*, a foreign herbaceous species, is the first plant successfully to invade those localities where the wet, compact soil, covered with salt incrustation, does not exceed a pH of 8.4. There are still many barren areas where the soil exceeds a pH of 8.4 due principally to the abundance of sodium carbonate. *Sporobolus vaginaeflorus*, a native grass, is the original pioneer in those areas where salt incrustations are absent and the reaction is less than pH 8.4. Here is an interesting case where the hydrogen-ion concentration is a limiting factor in the distribution of both *Linaria* and *Sporobolus*, and the salt incrustations set up a sharp boundary between the two species.

Competition begins in the initial pioneer stages when *Linaria minor* by organic deposition introduces certain edaphic conditions which are favorable for the invasion of *Sporobolus vaginaeflorus* and two foreign species, *Salsola kali* and *Tussilago farfara*. *Salsola* and *Tussilago* seldom play an important role in such poorly drained habitats but *Sporobolus* completely replaces *Linaria* as it extends its range to other areas.

¹ All data presented in this paper are averages of 8 quadrat determinations taken in different areas which were similar in physical characteristics.

TABLE I. *List of plant species growing in the saline region*

	Native Country
<i>Herbs</i>	
<i>Ambrosia artemisiifolia</i> L.	America
<i>Anaphalis margaritacea</i> (L.) B. & H.	Asia
<i>Apocynum nemorale</i> Bernh.	Europe
<i>Arctium minus</i> (G. S. Miller) Fernald.	America
<i>Asclepias syriaca</i> L.	America
<i>Asclepias incarnata</i> L.	America
<i>Aster laevis</i> L.	America
<i>Aster novae-angliae</i> L.	America
<i>Aster paniculatus</i> Lam.	America
<i>Cirsium arvense</i> L.	Europe
<i>Cirsium muticum</i> Michx.	America
<i>Convolvulus sepium</i> L.	Europe
<i>Daucus carota</i> L.	Europe
<i>Dipsacus sylvestris</i> Huds.	Europe
<i>Hieracium aurantiacum</i> L.	Europe
<i>Hieracium florentinum</i> All.	Europe
<i>Lappula echinata</i> Gil.	Europe
<i>Linaria minor</i> (L.) Desf.	Europe
<i>Linaria vulgaris</i> Hill.	Europe
<i>Melilotus alba</i> Dear.	Europe
<i>Nepeta cataria</i> L.	Europe
<i>Oenothera biennis</i> L.	America
<i>Salsola kali</i> L.	Eurasia
<i>Solidago altissima</i> L.	America
<i>Solidago nemoralis</i> Ait.	America
<i>Sonchus arvensis</i> L.	Europe
<i>Sonchus oleraceus</i> L.	Europe
<i>Verbascum thapsus</i> L.	Europe
<i>Tussilago farfara</i> L.	Europe
<i>Grasses</i>	
<i>Agropyron repens</i> (L.) Beauv.	Europe
<i>Agrostis alba</i> L.	Europe
<i>Agrostis palustris</i> Huds.	Europe
<i>Dactylis glomerata</i> L.	Europe
<i>Elymus virginicus</i> L.	America
<i>Hordeum jubatum</i> L.	America
<i>Muhlenbergia uniflora</i> Muhl. Fernald.	America
<i>Panicum capillare</i> L.	America
<i>Panicum huachucae</i> Ashe.	America
<i>Poa compressa</i> L.	Europe
<i>Poa pratensis</i> L.	Eurasia
<i>Sporobolus vaginatiflorus</i> (Torr.) Wood.	America

Sporobolus, Hordeum and Lappula Stage

The first stage of the succession introduced the following physical and chemical changes in the upper inch of the soil. The pH decreased from 8.4 to 8.1, the chloride content decreased from 1200 to 680 p.p.m., and the organic matter increased 11 per cent according to ignition determinations.² To what extent leaching in the soil may account for these differences is not known, which fact is true of all determinations of this investigation.

The above soil changes introduced an environment favorable for the in-

² The soil of this region is high in calcium, therefore the ignition values are slightly higher than in soils low in this element.

vasion of *Hordeum jubatum*, a native grass, and *Lappula echinata*, a foreign herb with root system extending approximately two inches below those of *Sporobolus*. These are followed by two foreign species, *Sonchus oleraceus*, *S. arvensis*, and *Ambrosia artemisiifolia* a native with still deeper (6 inches) root systems. Competition in this stage becomes very pronounced and *Hordeum* suffers a high mortality while approximately one-third of the *Sporobolus* population, based upon quadrat data, is eliminated because the soil level in which their roots grow is also occupied by the secondary roots of the more recent arrivals.

Hieracium, Daucus and Aster Stage

The reactional effect of the plants in the stage just described was primarily edaphic, since the organic content increased 5 per cent in the upper two inches of the soil as compared with the first original stage and the chloride content was reduced approximately 30 per cent while the pH decreased from 8.1 to 7.8. These are pronounced changes considering the short time the successional forces have been in operation. At this time the environment becomes favorable to the ecological demands of *Aster laevis*, a native plant, *Hieracium florentinum* and *Daucus carota*, two Old World species, to obtain a foothold in the community. Figure 1 shows the relative position of these plants in a very

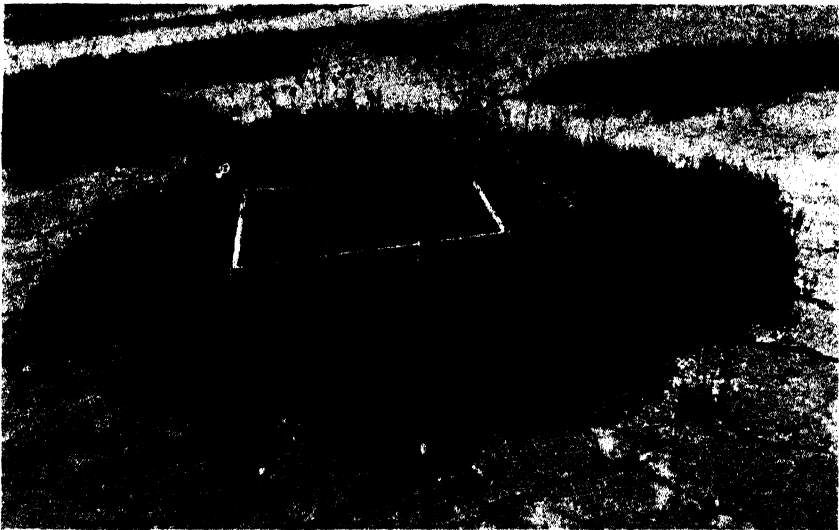


FIG. 1. A very small area showing the positions occupied by *Aster laevis*, *Hieracium florentinum*, and *Daucus carota* in relation to the advance of the succession.

small habitat which is also representative of their distribution in larger areas. The position of the root systems is represented in figure 2 and points out in a striking manner the ability of these plants to adjust themselves to the community by a gradient root penetration which enables them to regulate competition and at the same time receive sufficient nutrients from the soil for

normal growth. A seasonal foliage growth sequence is also perfected by these plants since *Sporobolus* and *Hordeum* complete their early growth before the shade of the two *Sonchus* species and *Lappula echinata* become effective, and these in turn make sufficient growth to insure maturity before the more



FIG. 2. Bisect showing root and top habits of the plants comprising the *Hieracium*, *Daucus* and *Aster* stage. 1, *Hieracium*; 2, *Sonchus*; 3, *Hordeum*; 4, *Daucus*; 5, *Sporobolus*; 6, *Ambrosia*; 7, *Lappula*; and 8, *Aster*.

bulky forms of the other species are completely developed. Thus a social relationship, incident to competition, becomes apparent both from above and below the surface of the soil.

Aster, Solidago and Daucus Stage

In this stage the native and foreign plants are practically equal as to number of species, and theoretically, the plants create a congenial environment and dominance lies in the balance. A slight environmental change, however, completely upsets this apparent equilibrium among the various species and a severe type of competition follows, as *Anaphalis margaritacea*, a foreigner, and *Solidago nemoralis*, *Asclepias syriaca* and *A. incarnata*, native species, secure a foothold in the habitat. As the reactional processes continue, a dominance which includes *Aster laevis*, *Solidago nemoralis* and *Daucus carota*,

becomes apparent. The surface inch of soil now reveals the following values: Organic matter 19 per cent, chloride content 260 p.p.m., and pH 7.2. The upper three inches of soil becomes highly flocculated and seeds of numerous species other than those of the community germinate but are either unable to compete for the soil nutrients or to tolerate the environment beyond the early seedling stage. Even *Salicornia europaea* and *Spergularia media*, two salt-loving species found abundantly on the northeastern shore of Onondaga Lake, where the old salt (NaCl) vats were located, have not as yet successfully invaded the saline areas because of the toxic effect of calcium chloride content associated with the low soil moisture content. Such evidence was obtained from seed planting of these species in several areas where the seedlings died soon after germination. Mosses and lichens are also absent from the region which is undoubtedly due to toxic effects of the soil.

Agrostis alba, *Poa compressa* Stage

Hordeum drops out completely during this stage and approximately 75 per cent of the *Sporobolus* population is replaced. A few individuals of

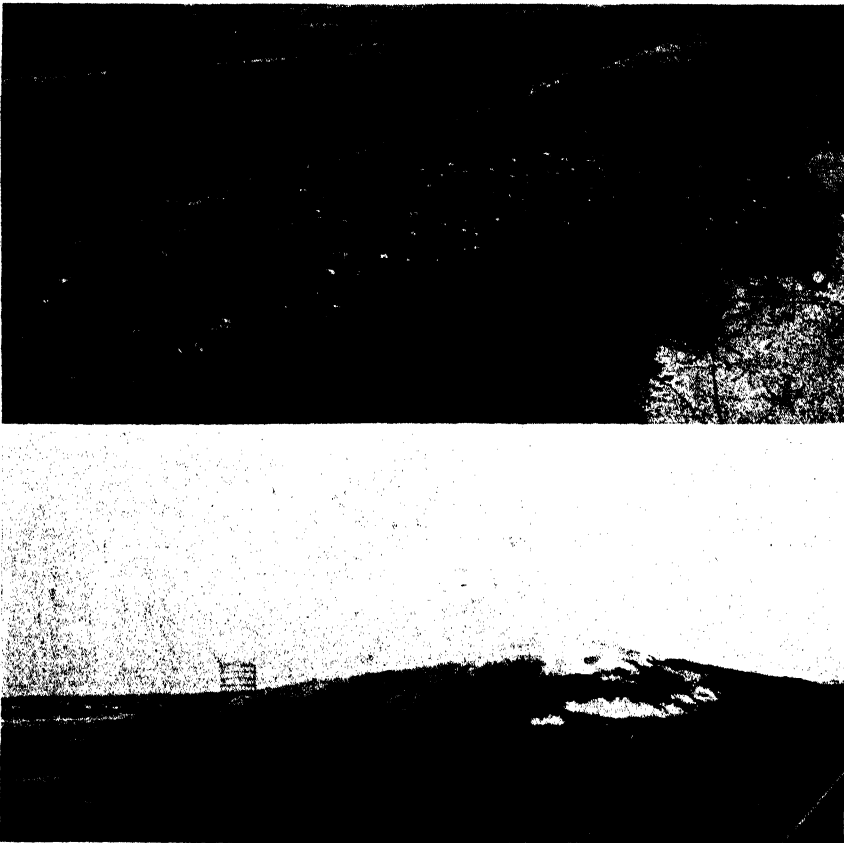


FIG. 3. *Poa compressa* replacing *Anaphalis margaritacea* (above).

FIG. 4. The northwestern footslope showing a dense grass community which forms the edaphic climax of the region (below).

Lappula, *Sonchus*, *Ambrosia* and *Asclepias* are able only to survive the new environment. *Hieracium florentinum* and *Anaphalis margaritacea*, with deep-spreading root systems are the most persistent of the non-dominants but they ultimately give way to *Poa compressa* and *Agrostis alba*, two grasses introduced from Europe, which form the edaphic climax of the region. An illustration of this is emphasized in figure 3 where *Poa compressa* is invading an *Anaphalis* colony. Here these two species with abundant rootstocks as part of their underground systems set up a stubborn competitive struggle for space both above and below the surface of the soil. As observed elsewhere, *Poa* will ultimately establish dominance because of the larger number of individual plants grown from one root system as compared to the few individuals supported by that of *Anaphalis*.

As *Agrostis alba* and *Poa compressa* enter this stage of the succession, the following grasses also find the environment suitable for growth in very limited numbers: *Dactylis glomerata*, *Panicum huachucae*, *Agropyron repens*, and *Sporobolus uniflorus*. *Apocynum nemorale*, *Oenothera biennis* and *Cirsium muticum* grow sparingly where the humus content is relatively high.

RESULTS OF QUADRAT STUDIES OF THE VEGETATION ON THE FOOTSLOPES

The vegetational history of the succession along the footslopes is quite similar to that of the upland area just described. It is more advanced, however, in certain areas because it ranges from 2 to 6 years older according to the slope gradient. A dense growth of grasses (fig. 4) forms the edaphic climax on the footslopes along the lake shore under the influence of moisture laden winds. On the dry south exposed slopes the vegetation is much retarded. *Salsola kali*, the first pioneer of the succession, still forms dense growths along the summit of the lake front footslopes where the surface soil is dry and rich in alkali salts.

Vegetation of the Lake Shore Footslopes

These footslopes may vary in distance from 20 to 100 yards from the water line of Onondaga Lake.

Along the extreme northwestern footslope, a small area where the successional march has been slowed up is illustrated in figure 5, which now supports many of the plants characteristic of the early stages of the upland area, while *Agrostis alba* and *Poa compressa*, the dominant species of the footslopes, occupy the surrounding ground. *Poa compressa* is the more aggressive of the two dominant grasses and often forms comparatively pure stands in small areas. Here its network of roots and rootstocks grows in the soil to a depth of 12 inches and forces out all former plants. All of the grass species listed in table I, however, grow sparingly at certain points along the lake footslopes with *Elymus virginicus*, *Muhlenbergia uniflora*, and *Poa pratensis* confined to the bases of the slopes. The upper 6 inches of soil in this

stage closely approaches, through the various agencies of deposition and leaching, a highly flocculated loam with the following chemical composition.

Depth in inches	Organic matter	pH	Chloride
	%		p.p.m.
1	19.2	7.1	300
3	10.2	7.4	680
6	8.0	7.7	760
6-12	3.2	8.2	900

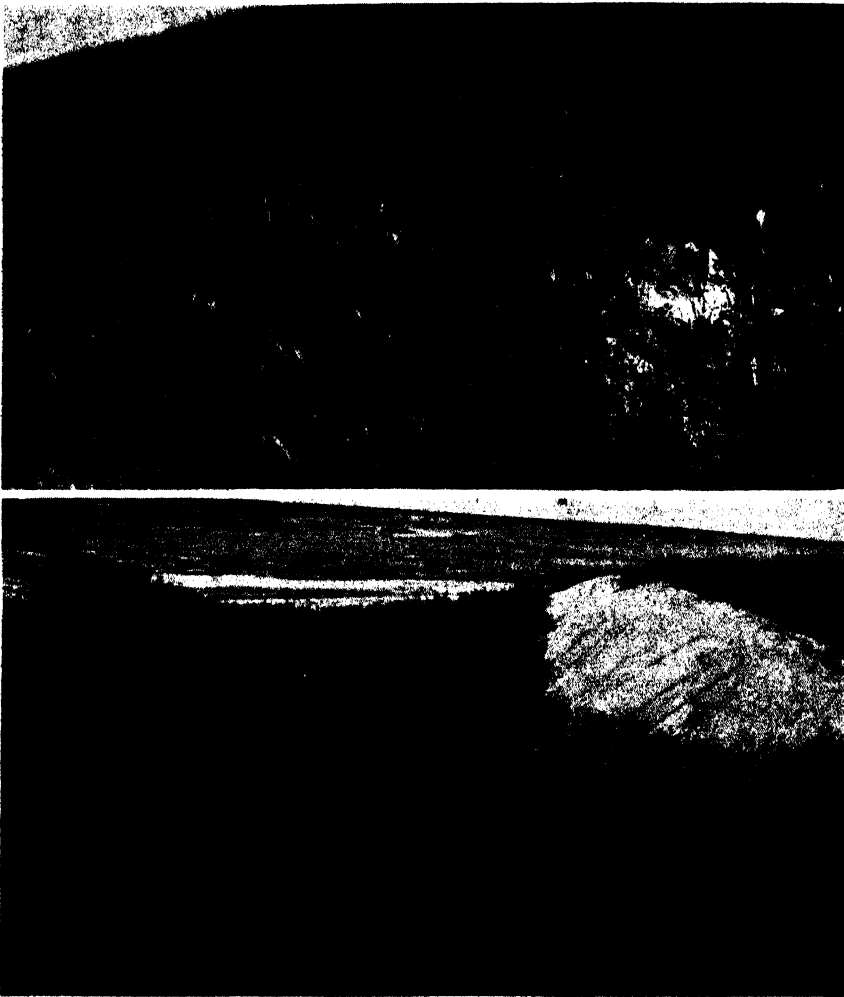


FIG. 5. A small place on the northwestern footslope where species characteristic of the early stages of the upland area are still evident (above).

FIG. 6. A highly developed cosmopolitan community in a small ravine (below).

Extending eastward along the footslopes, small terrace areas still support a rich cosmopolitan flora. *Solidago altissima*, *Aster laevis* and *Daucus carota* are the dominant species but *Agrostis alba* and *Poa compressa* are slowly

obtaining a foothold. Here *Solidago altissima* has replaced *S. nemoralis* in the better drained soil. Associated with these dominants are *Nepeta cataria*, *Melilotus alba*, *Linaria vulgaris*, *Arctium minus*, *Convolvulus sepium*, *Dipsacus sylvestris*, *Cirsium muticum*, and *Verbascum thapsus* of the Old World, and *Aster paniculatus*, a native of America. Several of these species are extremely limited in numbers, while others are quite abundant. At one point along the footslopes, a low terrace area approximately 12 feet wide and 200 feet long supports *Solidago altissima* as a single dominant which grows to the height of 4 feet. Notwithstanding its abundant foliage and a highly developed root system of numerous root-stocks, a few individuals of other species are able to survive the competition as indicated by the population count in table II which was made July 18 and September 10, 1933 in a one meter quadrat.

TABLE II. Showing the number of plants supported by a one meter quadrat

No. of plants July 18	Species	Appearance July 18	Total plants Sept. 10
117	<i>Solidago altissima</i>	30 dwarfed plants	90
33	<i>Melilotus alba</i>	Small plants	8
10	<i>Daucus carota</i>	8 small plants	2
8	<i>Agrostis alba</i>	Small plants	8
2	<i>Asclepias incarnata</i>	Small plants	1
4	<i>Aster laevis</i>	Small plants	3
4	<i>Aster paniculatus</i>	Small plants	1
5	<i>Poa compressa</i>	Small plants	5

With the exception of *Agrostis alba* and *Poa compressa*, all of the species listed in table II suffered a high mortality which is strong evidence that once the two grasses obtain a foothold they apparently persist. The chemical and physical analysis of the upper 6 inches of the soil shows 18 per cent organic matter which is the highest value obtained in the region while the chloride value and soil reaction, 130 p.p.m. and pH 7.0 respectively, are the lowest recorded. These data, together with the location of the area, clearly indicate that considerable leaching has occurred in the past and the habitat has become well suited for the growth of *Solidago altissima* and thereby it becomes a single dominant. This is another interesting case of plant distribution due to differences in soil composition.

VEGETATION OF THE RAVINES

Along the steep sides of the ravines the pioneers are *Tussilago farfara* and *Melilotus alba*, two foreign plants with deep roots well adapted to resist the effects of erosion. On the floor of the ravines (fig. 6) where the soil is a rich loam due to leaching and abundant organic deposition, the dominant species are *Solidago altissima*, *Aster novae-angliae*, and *Cirsium arvense*. The two former species are native but the latter is European. Mingling with these dominants are 6 species of foreign origin, namely, *Salsola kali*, *Tussilago*

farfara, *Melilotus alba*, *Daucus carota*, *Cirsium muticum* and a few plants of *Agropyron repens*. Associated with their height, bulk, and highly developed root systems is a seasonal growth development which has brought about a certain cosmopolitan sociological relationship so well balanced that all other invaders up to the present time have been unable to reach ecesis. It is highly possible that these species have become so well adapted through morphological and physiological specialization that the present type of vegetation may continue over a considerable period of time.

SUMMARY AND CONCLUSION

A cosmopolitan community of 29 herbaceous dicotyledons and 12 grasses in which 18 of the former and 6 of the latter are of foreign origin have successfully invaded a saline area near Syracuse, New York. These species are present not because of their mobility but due to their ability to tolerate the saline conditions of the area since numerous invading species each year never developed beyond the early seedling stage.

A certain degree of social relationship incident to competition becomes apparent among the foreign and native species from the initial pioneer stage to and including the edaphic climax.

Slight differences in the topographic features associated with small changes in exposure not only influence the rate of succession but also the species involved in the various stages of the succession.

A major result of the present investigation is the establishment by chemical and electrometric measurements of the fact that a definite gradient change in the physical and chemical composition of the soil is correlated with successional change.

This saline area apparently supports a selection of the most aggressive European and Asiatic plants known in the eastern world. They are obnoxious weeds of the undesirable type. Nevertheless it is highly possible many of our plants are equally as aggressive in other countries of the world and become equally obnoxious.

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TERRESTRIAL AND FRESH-WATER FAUNA OF THE MARQUESAS ISLANDS¹

EDWARD PHILPOTT MUMFORD

University of Chicago and University Museum, Oxford

INTRODUCTION

I propose in this paper to say something of a project, initiated in more prosperous times, and carried on, despite the depression, by a group of prominent and far-seeing business men and scientists in Hawaii. The classic work of R. C. L. Perkins ('13), has formed the basis of subsequent economic work that has saved the Hawaiian Sugar Planters millions of dollars. It was to some extent with this as an inspiration, that Dr. C. Montague Cooke, an international authority on Pacific land snail faunas and a Trustee of the Bernice P. Bishop Museum, and Dr. Arthur L. Dean, and Mr. John E. Russell and his associates, initiated the following researches some six years ago.

The object of their investigations, carried on in association with well-known entomologists like Dr. R. N. Chapman, Director of the Experiment Station of the Association of Hawaiian Pineapple Cannerys, and Mr. C. E. Pemberton, Executive Entomologist to the Hawaiian Sugar Planters' Association, and the forester, Mr. Charles S. Judd, was to collect and study the insects of the isolated and ancient Marquesas Islands (Mumford and Adamson, '33), both in relation to their environment—physical and biotic—and in comparison with other Pacific faunas.

Though the generally accepted theory is that the faunal migration waves originated on the western borders of the Pacific, gradually losing their force as they travelled eastward, ethnologists, zoologists, and botanists have long debated the possibility of some American influence coming from the opposite direction. The strategic position of the Marquesas, as the principal high islands near the eastern border of Polynesia,² promised results of great

¹ This paper, which was read before the Ecology Seminar of the University of Chicago, is based on the researches of the Pacific Entomological Survey, of which the author was appointed Director. The field work was undertaken in collaboration with A. M. Adamson, to whom grateful acknowledgment is here made.

² In the following pages I have employed the term "Polynesia," not to denote a zoogeographical entity, but, as used by the Bishop Museum, as a comprehensive term to include all of the islands inhabited by the race of that name. Thus, both New Zealand and Hawaii, though obviously separate provinces, have faunas of exceptional interest that have been studied for many years, and may be expected to yield interesting comparisons with those of the rest of Polynesia, with which they share a common language. In adopting such a course, I am perhaps unduly influenced by my interests in ethno-botany and ethno-zoology, which I feel have important contributions to make to the problems of distribution.

interest, prompting as they did R. C. L. Perkins' prediction (*in litt.*) that they might well prove to be "the choicest part of the oceanic islands of the Pacific after Hawaii."

It is generally recognized that the inestimable importance of the *Fauna Hawaiiensis* as a contribution to scientific knowledge lies in the fact that, besides describing a fauna of exceptional interest to the systematic zoologist, it embodies the results of Perkins' brilliant investigations on the relation of that fauna to its environment. For this reason, those in charge of the work, in consultation with Mr. O. H. Swezey and other experts, constantly stressed the importance of obtaining precise data regarding localities, altitudes, host-plants etc. In the field, however, we were confronted with an almost complete dearth of published information of this nature, so essential as a background to entomological research. The names of collecting grounds became meaningless as the published charts indicated little more than the coast-line, leaving most of the interior blank; and the knowledge of many of these native place names appeared to be confined to a few of the older natives. In a similar way, practically nothing had been published on the Marquesan host-plants, and it was necessary to collect large series of these, for the accurate determination of which we are indebted to Dr. E. D. Merrill, Director of the New York Botanical Gardens. As a rule, the more important endemic insects are taken in association with native plants and are restricted to high altitudes. Such data are, therefore, of some assistance in estimating the probable status of such insects as have to be described as new. Altitudes were taken with Paulin altimeters.

In attempting to describe the physical environment as a whole, as compared with the precise habitat of the individual species, it seemed desirable to initiate the taking of some elementary meteorological observations. These have since been worked up by Professor John B. Leighley ('33); and carried on by the National Research Council. Extensive notes were also taken with a view to describing the topography, and observations were made bearing on the geological history.

In studying the Marquesan insects in relation to other faunas, it was necessary to make fairly extensive researches into the literature, and a card catalogue of thousands of references has been compiled for this purpose. This is constantly being revised and brought up to date in consultation with appropriate specialists. At this point it seems appropriate to make some acknowledgment of the enthusiastic cooperation that I received from associates in Chicago like Dr. Alfred E. Emerson of the University, and Mr. Karl Schmidt of the Field Museum, and also to thank those ecologists who have patiently waded through our final report, like Dr. R. N. Chapman and Professor W. C. Allee. For a careful revision of the native names, I am indebted to Dr. E. S. Craighill Handy, Ethnologist to the Bernice P. Bishop Museum. Dr. Handy was in the Marquesas in 1920-21 as a member of the Bayard Dominick Expedition.

A factual report on the insects and related organisms, and a description of the physical environment, is being published elsewhere, but as zoogeographical conclusions drawn from any one group are notoriously open to question, I have taken the opportunity of summarizing here what is known of the rest of the fauna.

It should, however, be clearly borne in mind that studies other than entomological were subsidiary, and that collections in other groups of animals were made only incidentally. For this reason, it is particularly important not to assume that what was not taken was necessarily not present, and it also seemed advisable to include some mention of other records from Polynesia.

REVIEW OF THE FAUNA

Of the seven phyla now known to be present in the Marquesan terrestrial and fresh-water fauna, four—the Platyhelminthes, Arthropoda, Mollusca, and Chordata—may include an endemic element; two—the Rotifera and Annelida—are perhaps not native, though the former may be partly of Polynesian introduction; and one—the Nemathelminthes—occupies a more doubtful status. One more—the Protozoa—or two more—if we include the Acanthocephala—doubtless occur, and may include autochthonous species. A tenth—the Polyzoa—has been taken in fresh-water in Polynesia only from the Society Islands, and the eleventh—Nemertinea—does not appear to range east of Samoa. Fresh-water Porifera and Coelenterata, though not yet recorded in the literature from Polynesia east of Fiji, may perhaps turn up later, but the others—Ctenophora, Chaetognatha, Phoronidea, Echiuroidea, Sipunculoidea, Priapulioidea, Brachiopoda, and Echinodermata—may be eliminated from the discussion as including only marine forms.

PROTOZOA

Most free-living Protozoa are "cosmopolitan, and the temptation to describe new species because they happen to have been found in some hitherto unexplored locality has no justification from the facts of geographical distribution" (Calkins, '21). This is particularly applicable to the fresh-water species. Many of the parasitic forms, on the other hand, may be confined to a single species of host, and if this should be autochthonous, they may be restricted correspondingly in their range. Arrangements are being made to study the flagellate fauna in the intestines of some of the Marquesan termites, several species of which are thought to be peculiar to this archipelago. Preliminary studies have already been made on the Protozoan intestinal fauna of the Hawaiian termites. Some fresh-water Protozoa have also been listed from Samoa, Hawaii, and the Society Islands.

PORIFERA

Fresh-water sponges have never been recorded in the literature from Polynesia east of Fiji, the type locality of *Spongilla gilsoni*, though, as Dr. N.

Gist Gee (*in litt.*) tells me that the "gemmules may be readily carried by birds or strong winds over long distances, or they may be lodged inside of cracks in floating pieces of wood or other debris, and thus carried for long distances," they may perhaps be expected to turn up later. Marine forms are known to the Marquesans as *paatai* or *paatai moana*.

COELENTERATA

I know of no published records of fresh-water hydroids from Polynesia outside New Zealand, with its cosmopolitan *Hydra viridis*, and its introduced *Cordylophora lacustris* var. *otagoensis*. We did not take any in the Marquesas, but they are said to occur in Hawaii.

PLATYHELMINTHES

The discovery in the Marquesas of two new species of *Geoplana* was of some interest, as the terrestrial flatworms have been much discussed in connection with the theories of continental connections. One of the species was taken in wet humus at nearly four thousand feet at Matauuna, Hivaoa, and the other was collected just over seventeen hundred feet on Uahuka.

In addition to *Rhynchodemus putzei*, originally described from the islands in 1899, and again taken by us under dead leaves on the ground in the cloud zone at Matauuna, a further undescribed species of the same genus was taken from two thousand feet upwards on Nukuhiva.

A further species of flatworm, *Platydesmus quadristriatus*, was described from Tonga in 1868, but the only terrestrial form reported from Samoa and Hawaii is the cosmopolitan *Placocephalus kewense* also taken in Tonga.

Fresh-water Planarians were not found in the Marquesas, but I understand that one or two species, as yet undetermined, have been seen in Hawaii.

Von Ihering ('02) and Johnston ('13) have considered the bearing of parasitic trematodes on past land connections, and it is possible that material for similar studies might be collected in the Marquesas, where the only record that we have, as yet unpublished, is of the eggs of a fluke resembling *Paragonimus westermanii* isolated from a Marquesan at Hatiheu, Nukuhiva. Other species of comparatively little interest from the standpoint of distribution, have been listed from Hawaii. I know of no records of forms peculiar to Polynesia proper.

Some of the autochthonous Marquesan land birds may harbour peculiar species of tapeworm like the Hawaiian *Drepanidotaenia hemignathi* on the endemic *akialoa* (*Hemignathus procerus*), and the peculiar New Zealand *minuta* and *apterygis* on the endemic *kiwi* (*Apteryx*).

A collection of over thirteen hundred specimens of fresh-water Crustacea is to be searched for epizooic Temnocephaloidea. They do not appear to have been recorded from Polynesia, but there is no apparent reason why they should not occur.

NEMERTINA

Terrestrial unsegmented worms are unknown from Polynesia east of Samoa, which supports *Geonemertes palaënsis* coming from the East Indies. In New Zealand, to the west, there is the supposedly endemic *novae-zelandiae*, and from the Auckland and Enderby Islands we know of *spirospermia* and *caeca* respectively. None was found in the Marquesas.

NEMATHELMINTHES

Until more is known of the "round worms" (Nematoda) of Polynesia east of Fiji, little can be said regarding their supposed status in these insular faunas. Free-living nematodes were seen in the Marquesan cloud zone, and such forms have been described from low levels in Hawaii.

Among immigrant parasitic species determined from the Marquesan collections to date, mention may be made of *Ascaris lumbricoides* known to the natives as *potu* (cf. the Tongan *botu*) or *potiveo*, and possibly not of such recent introduction as suggested for elsewhere in Polynesia by Lambert ('28); *Enterobius vermicularis* known to the natives as *kaio* or *naio* (cf. the Hawaiian *naio*) and more rarely as *matio* or *matiko*; *Rhabditis coarctata* numerous adults and cysts of which are commonly found attached to the larva of an as yet unidentified Eucosmid; and the lungworm, *Metastrongylus clongatus*. Moreover, if filarial infection is an essential precursor of elephantiasis, then these worms (*Wucheria bancrofti*) are present in the Marquesas, where, in its manifest form, the disease is known as *feŋe* or *hehe*. Unlike the rest of Polynesia, where P. A. Buxton ('27-8) considers that "filariasis (and elephantiasis?) has been prevalent from time immemorial," this disease is believed by the natives and residents to be of fairly recent introduction into the Marquesas. The naturalist Frederick D. Bennett ('40), who visited the group in the latter part of 1833, commented upon the total absence of elephantiasis, and it is generally considered that the disease first reached Uahuka within comparatively recent times with some convicts from Raiatea in the Society Islands; it is now wide-spread throughout the group. What may well have been Manson's eye worm, *Oxyspirura masoni*, has been taken on fowl.

ACANTHOCEPHALA

Peculiar species of Acanthocephala, a group with rather doubtful affinities, may perhaps be expected to occur in the alimentary canals of some of the land birds restricted to the Marquesas. In Hawaii, we have *Apororhynchus hemignathi* on the autochthonous *akiāloa* (*Hemignathus procerus*), and in New Zealand an undescribed *Echinorhynchus* has been taken in the intestine of the endemic *kiwi* (*Apteryx*).

ROTIFERA

Dr. Chancey Juday of the University of Wisconsin found no rotifers in the samples of fresh-water Plankton submitted to him for study, but I understand that my colleague, A. M. Adamson, found them in a temporary pool, Vaihakameama, at about two thousand six hundred feet in western Toovii, Nukuhiva. A number of species have been listed from New Zealand, Samoa, and Hawaii.

ANNELIDA

Archannelida have, as far as I am aware, never been recorded from Polynesia. The older view that they are really primitive forms is no longer generally held. Despite this fact the discovery of terrestrial or fresh-water forms in this region would be of considerable interest.

Though we did not find any fresh-water "bristle-worms" (Polychaeta) in the Marquesas, *Perinereis seurati* has been described from Taraouroa, off Aukena, Mangareva, and *Lycastis hawaiiensis* from Hawaii. *Lycastis quadriceps* is known from Campbell Island, New Zealand.

As far as the Oligochaetes are concerned, only two species—the circum-tropical *Pontoscolex corethrurus* and the Australian *Megascolex tenax*—have been listed from the Marquesas, and of these, the latter record seems doubtful; the specimen upon which it is based is in the Berlin Museum, and was originally described by Michaelsen in 1892 as *Perichaeta albida* with the notation "angeblich von Marquesas de Mendoza"; in 1900 he placed *albida* in synonymy with *tenax* with an Australian distribution, prefacing the "Marquesas de Mendoza" with a question mark.

Though the Marquesan collections, made on all of the inhabited islands, and on Eiao and Mohotani, from sea level to the highest altitudes, have not yet been finally determined, endemic oligochaetes are perhaps hardly to be expected. As a tentative hypothesis, it may be suggested that some of the earthworms were of aboriginal introduction, arriving with the Polynesian and his food-plants somewhere around the tenth century, and that others came with the more extensive introductions of the white man. In this connection, it is perhaps of interest to note that the Marquesan native name for earthworm, *noke* or *noe*, *toke* or *toe*, is found throughout the region under consideration, these Oligochaetes being known to the Maoris as *noke* or *toke*, to the Rarotongans as *toketoke*, to the Tahitians as *toe*, to the Mangarevans as *iritoke*, to the Tuamotuans as *toke*, and to the Hawaiians as *koe*. No terrestrial oligochaetes were taken on the isolated and uninhabited islands of Hatutaa and Fatuuku.

The presence of a fresh-water form, doubtless widespread, in Lake Vaihira, Tahiti, is of interest as the first record of such a species from Polynesia proper.

With regard to the leeches (Hirudinea), it is interesting to note that though we did not take any in the Marquesas, and the natives, and residents

seemed convinced as to their absence, Dordillon ('04) gives a native name *toke omo toto* for "sangsue," and that W. A. Bryan ('15) says that "two species (of leech) are quite common in the streams of Oahu, and there are doubtless other species in the other (Hawaiian) Islands." A fresh-water form, *Glossiphonia (Clepsine) novae-zealandiae*, has been described from New Zealand, where there is a doubtful record of the terrestrial *Geobdella limbata*, and *Philaemon minutus* is not known outside of its type-locality, Samoa.

ARTHROPODA

Onychophora

Other than the three species of *Peripatoides*—*novaezealandiae*, *suteri*, and *viridimaculatus*—described from New Zealand, no members of this ancient class appear to have been recorded from "Polynesia," though Austin H. Clark ('15) includes Samoa among groups "where almost certainly they occur," and unidentified species are said to have been met with as far east as Fiji. Their absence from the Marquesas is, therefore, not surprising.

Chilopoda and Diplopoda

Unlike New Zealand, Samoa, Hawaii, etc., there do not appear to be any autochthonous centipedes or millipedes in the Marquesas. Even the *vei enata* or *vei maoi*, the so-called "native centipede," now on the verge of extinction, proved to be wide-spread.

Pauropoda

No native pauropods have been described from "Polynesia," but a few supposedly introduced forms, less than a millimeter and a half long, have been taken in Hawaii.

Symphyla

The only representative of this primitive class taken in the Marquesas was the wide-spread *Hanseniella orientalis* previously known to range from Siam and the East Indies as far as Samoa. Endemic forms are unknown from "Polynesia" outside of New Zealand, the type-locality of *neozelanica*. Introduced forms have also been taken in Hawaii.

Insecta

Of the eighteen orders of insects, representative series of which were taken in the Marquesas, three may be dismissed as obviously not native *viz.* the earwigs (Dermaptera) with peculiar species in New Zealand (?), Samoa, and Hawaii; the archaic "webspinners" or Embioptera, said to be absent from New Zealand, but with a doubtfully native species in Hawaii; the fleas (Siphonaptera) with a supposedly peculiar species, *Xenopsylla hawaiiensis*, in Hawaii; and the sucking lice (Anoplura). Thirteen more orders—the silverfish or bristle-tails (Thysanura), the springtails (Collembola), the

dragon-flies (Odonata), the Orthoptera, the termites (Isoptera), the psocids (Psocoptera), the thrips (Thysanoptera), the "bugs" (Hemiptera and Homoptera), the beetles (Coleoptera), the Hymenoptera, the Neuroptera, Diptera, and the butterflies and moths (Lepidoptera)—include forms not known elsewhere and perhaps endemic.

Of the seven orders not yet taken in the Marquesas, the minute Protura^a have been found in New Zealand and Hawaii; the may-flies (Ephemeroptera) and the caddis-flies (Trichoptera) have been recorded from New Zealand and Samoa; the Zoraptera have been discovered recently in Samoa and Hawaii, and doubtless occur in New Zealand, though they have not yet been taken there; the Strepsiptera are as yet reported only from Hawaii in Polynesia; and the stone-flies (Plecoptera) and the scorpion-flies (Mecoptera) are unknown from "Polynesia" outside of New Zealand.

Arachnida

Of the ten living orders of this class now recognized, one—the Xiphosura—now includes only marine forms which have not reached Polynesia. Of the other nine, all but two—the Ricinulei and Solpugida (Solfugae, Galeodea)—occur in "Polynesia."

Three of the four Polynesian orders which have succeeded in reaching the Marquesas are represented in the endemic fauna, namely the Araneida, Chelonethida (Pseudoscorpionida), and Acarina, but the fourth—Scorpionida—is, as elsewhere in Polynesia, represented only by one or more introduced forms.

Of the three orders known from elsewhere in Polynesia, but possibly absent from the Marquesas, the Pedipalpida have supposedly peculiar species in New Zealand and Samoa; the Microthelyphonida (Palpigradi) include an undetermined species of micro-whip-scorpion recently discovered in Hawaii; and the Phalangida include one or more New Zealand species of soft-bodied harvestmen.

Crustacea

Of the five sub-classes of Crustacea, not more than four—the Ostracoda, Copepoda, Cirripedia, and Malacostraca—are represented in the Marquesan fauna, and one of them—the Cirripedia—does not fall within the scope of this report, as it is almost exclusively marine, only one or two species penetrating a little way into estuaries. The fifth sub-class—Branchiopoda—is presumably present in the Marquesas, as in many other parts of Polynesia, though specimens have not yet been taken there. For the moment, I shall only consider two of these sub-classes.

Ostracoda:

Cypretta nukuhivana (the females of which were discovered presumably reproducing parthenogenetically at about two thousand six hundred feet in

^a Minute organisms were collected under lens and binocular. A Berlese funnel was not used in the Marquesas.

Vaihakameama pond, Nukuhiva) though described from our collections as new, may perhaps be expected to turn up elsewhere.

Malacostraca :

At the moment, I can discuss only two—the Peracarida and Eucarida—of the five main divisions of this class, and in these I can only touch upon three orders, the isopods, amphipods, and decapods. Of these latter, the first two contain species not known elsewhere, and perhaps autochthonous, and the third includes the Atyidae, which Ortmann ('02) considers as one of the oldest groups of fresh-water decapods, possibly originating in the Jurassic, and which is of some interest as perhaps lending support to Meyrick ('28) and Poulton and Riley's ('28) assumption that the Marquesas are the remnants of some old and extensive land mass.

Tardigrada

"Bear animalcules" are amongst the most minute animals known to exist, the largest not being much over a millimeter in length, and most of them being very much smaller. Had a special search been made for them in the Marquesas, they would doubtless have been discovered.

When so little is known of these minute organisms, which are readily distributed by wind, it is unwise to speculate as to the origin and affinities of Polynesian forms. It is, however, perhaps of some interest to note that the Samoan *Macrobiotus samoanus* is not known elsewhere, and that the New Zealand *Echiniscus velaminis* and *Macrobiotus montanus* have been recorded only from an altitude of six thousand feet on Nun's Veil Mountain in the Mount Cook district of the same Province. None of the species determined from Hawaii to date, however, appear to be endemic.

Pentastomida (Linguatulida)

Only two species of pentastomid—*Alofia ginac* and *A. (?) merki* described from an unrecorded host in Samoa—appear to have been listed from Polynesia, though a further species—*Waddycephalus vitiensis* Heymons also from an unrecorded host—has been described from Fiji. None of this group of uncertain systematic position was taken in the Marquesas, though representatives may perhaps occur there.

MOLLUSCA

Land-snails supply important evidence regarding ancient faunal relations. Thus Pilsbry ('00) points out that the genus *Partula* (of which we discovered an endemic sub-genus with eighteen or more peculiar species in the Marquesas) is wide-spread through Melanesia and Polynesia, and that it is an ancient generalized type not found elsewhere. On the other hand, many groups of land-snails wide-spread elsewhere are absent from Polynesia proper, though known to be able to colonize oceanic islands in other parts of

the world. Throughout this region, the snail fauna is remarkably uniform, though unlike that found anywhere else. From this, and other facts, Pilsbry, concludes there was once a continental mass including all of Polynesia, with Hawaii, but not, of course, New Zealand.

Our Marquesan collections of land-snails are at present in the hands of Dr. C. Montague Cooke of the Bishop Museum in Honolulu. As I understand it, the autochthonous species are distributed among: Zonitidae, Endodontidae, Pupillidae, Partulidae, Tornatellinidae, Succinidae and Helecinidae.

Only four fresh-water species were found, the *pipitaa*, *Neretina* (*Clithon*) *souleyetiana*, *Navicella* *apiata*, and two species of *Melania*, known to the natives as *pipihoaka*. Only the last of these was taken at high altitudes, and may perhaps be autochthonous. The *Navicella* was taken in company with the introduced isopod *Ligia vitiensis* taken on the wet cliff at the falls about a quarter of a mile up the Vaituha stream, Eiao, and the *Neretina* is abundant only at low levels.

POLYZOA

Though we did not take any fresh-water Polyzoa in the Marquesas, we found the cosmopolitan *Plumatella emarginata* in Lake Vaihira, Tahiti, the type locality of the apparently peculiar *Hyalina vaihiriae*. Outside of these records from the Society Islands, the only species known from "Polynesia" are *Fredericella sultana*, *Plumatella alpinii*, *P. princeps*, and *Paludicella articulata* from New Zealand. They have not been recorded from Hawaii or Samoa.

CHORDATA

Pisces

Though I have not yet had a chance to go into the literature in any detail, I think that I can safely state that none of the truly oceanic islands of Polynesia has strictly fresh-water fish, and, by that, I mean groups that were derived in such remote times that they have at present no very definite connection with any marine form. With the exception of the goby *Sicyopterus marquesensis* known only from its type locality, Omoa Valley, Fatuhiva, all of the fresh-water fish that we collected in the Marquesas are known elsewhere, and even this species may be regarded as a fairly recent derivative from a marine form. *Bryanina inana*, though described from our collections as a new genus and species, includes both the Society and Marquesas Islands within its range.

Amphibia

According to Barbour ('23), "the Fijian frogs occupy the extreme outposts to which amphibian migration in the Pacific has reached." They have, however, been artificially introduced by man into Hawaii, the Society Islands, and perhaps Samoa and Tonga. We did not see any in the Marquesas, and were given to understand that the translation of "grenouille" into *rana* in

Dordillon's dictionary was due to the missionaries' attempt to relate the story of the invasion of frogs into Egypt at the time of the Pharaohs. The name *rana* is used also in Tahiti. In Samoa, I am told that they are known as *lane*, and in Tonga they are called *boto*. I rather doubt whether they are thoroughly established outside of Hawaii, where they were first introduced some time prior to 1887.

Reptiles

As we are confining our discussion to the terrestrial and fresh-water forms, only passing reference can be made to the marine turtles, which come ashore from time to time. According to native informants, the Marquesans recognize three forms—the *honu*, the *honu kea* and *hono ueoa*—and these are perhaps comparable to the Hawaiian *honu* and *ea*. Mention of these sea turtles is commonly made in the native legends. Jardín ('58), who visited the Marquesas in 1854, recorded the Pacific green turtle (*Chelonia japonica*) and Louis Rollin ('29) more recently lists *Eretmochelys squamosa*. The Galapagos land-tortoises left on Tahuata in 1813 by David Porter ('23) do not appear to have become established.

Turning from the Testudinata to the Squamata, it is perhaps of interest to note that all of the Marquesan lizards—that is if we accept Brongersma's ('32) reduction of *Hemiphyllodactylus leucostictus* to a synonym of the Javanese *typus*—extend clear across the Pacific, and even into the New World. Previously known only from its type locality on Kauai in the Hawaiian Islands, we found it up to nearly three thousand feet in the Marquesas. The stumptoed gecko, *Peropus mutilatus*, for example, has become established in southern Mexico, the azure-tailed skink, *Emoia cyanura*, has been collected on Clipperton Island, and the snake-eyed skink, *Ablepharus boutonii peocilopleurus* has been taken from islands off the west coast of Ecuador and Peru.

The fact that these lizards are commonly mentioned in the ancient legends, that they appear to have a common native name throughout Polynesia, and that they were recorded as already present in the Marquesas by the early white explorers, suggests that some at least of the geckoes are of aboriginal introduction. Indeed, when reporting on Hawaiian lizards, Snyder ('19) writes that "wherever large canoes were seen lying on the beach (a number of them were carefully examined), geckoes were found among the mats covering them. Eggs were found also in the canoes. It would be quite impossible at the present time to provision and launch a canoe without including both adult geckoes and their eggs." Whether or not the Polynesians reached the Americas, or the lizards found their way there unaided, is a matter that I do not feel competent to discuss. To the Maoris, Tongans, Mangaian, Tuamotuans, and Marquesans, field skinks are known as *moko*. In the same way, the nocturnal geckoes called *kakaa* and *nanaa* by the Marquesans are known to the Maoris as *ngara* and the Tahitians as *arara*.

There are no snakes in the Marquesas, despite Vincendon Dumoulin and Desgraz's ('43) reference to "un petit boa long à peine de deux pieds, et qui doit former un genre nouveau" in 1838. The presence of the native name *puhi fenua* for "serpent" in Dordillon is probably due to the necessity of the early missionaries translating the story of the Garden of Eden. Terrestrial snakes are unknown from Polynesia east of Samoa, where *Enygrus australis* occurs as an entrant from the Solomons, Santa Cruz and the New Hebrides.

Birds

In addition to the widely distributed reef heron or *matuku* (*Demigretta sacra*) and the Tahitian rail or *koao* (*Porzanaidea nigra*), the Marquesan land birds include a species of swift (*Collocalia ocista*) and kingfisher (*Todiramphus tutus*), known to the natives as *kopeka* and *pahi* respectively, and restricted to the Marquesas and Society Islands; four or five species of endemic pigeon; an autochthonous parakeet, *Coriphilus ultramarinus*, known as the *pihiti*; three endemic fly-catchers of the Polynesian genus *Pomarea*, called *komao* or *omao taifa*. The endemic pigeons include the remarkable genus *Serresius*, known only from its type locality on Nukuhiva, where it is called the *upe*; the ground pigeons or *otue*, *Gallicolumba rubescens*, now restricted to the uninhabited islands of Eiao, Hatutaa, and Fatuuku, but according to native tradition once wide-spread through the group; and two or three species of fruit pigeon or *kuku* of the genus *Ptilinopus*.

The distribution of these birds is not haphazard. As in the brachyrhinine (otiorhynchine) weevils, the one endemic genus, *Serresius*, is confined to the island of Nukuhiva, which has a further species restricted to it. The autochthonous warblers and fly-catchers are divisible into sub-species, some of which do not extend their range over more than one island, except in the case of Hivaoa and Tahuata, which share the same species and may formerly have been connected.

Mammals

From the standpoint of distribution, the only Polynesian mammals of interest are those that have any claim to be considered as native, or of aboriginal introduction. I shall, therefore, consider only the bats, swine, rats, and dogs.

Though there are no bats in the Marquesas, the Polynesian name for these mammals—*kopea*, *opea*, *kopeka*, *kopekapeka*—persists, and is transferred to the swiftlet, *Collocalia ocista*, which resembles the bat in its manner of flight in the early evening, and in its habit of nesting in caves, and feeding on the wing. Chiroptera have been specifically determined from Tonga, Samoa, Hawaii, and the Society Islands, and perhaps range into the Cook Islands, where they receive the name *peka*.

Swine, probably descendants from a prehistoric native introduction, were

present in the Marquesas at the time of their discovery by the earliest white explorers. Fernandez de Quiros ('04) recorded them on Tahuata as early as 1595, and Captain James Cook and Johan Forster (1777-8), the naturalist who accompanied him, found them on the same island in 1774. In considering the possibility of a common origin for the Polynesian breed or race of swine, if such existed, it is of interest to consider the nomenclature for the pig throughout the different archipelagoes—to the Cook Islanders, Marquesans, and Tuamotuans, they are known as *puaka*; to the Maoris, Samoans, Hawaiians, and Tahitians as *puaa*; and to the Tongans as *buaka*.

Although the Marquesan *kioe cnata*, or "native rat," appears to have been present prior to the arrival of the earliest of white explorers, there is, as in the case of the *iole*, *Rattus hawaiiensis*, in the Sandwich Islands, no reason to suppose that their presence is due to other than human agency. As early as 1774, these rats were observed on Tahuata in the Marquesas by the naturalist Forster, who visited the islands on board the Resolution with Captain Cook. They were also noted on the same island by Etienne Marchand in 1791.

From the skins and skulls of *hawaiiensis*, the Marquesan specimens, as yet undescribed, appear to differ in slight but constant peculiarities, concerning whose meaning it is difficult to express an opinion in the absence of detailed knowledge regarding the Tahitian *iore*, described under the name of *exulans*, and the New Zealand *kiorc* described as *maorium*. The type of *exulans*, described in 1848, is still in the U. S. National Museum, but its present condition (much faded and without the skull), I am told, is such as to render it useless for taxonomic purposes.

A further search for races of the "Polynesian" rat might perhaps be made in the Cook Islands and Mangareva, where the name *kiorc* is still in use, and in Samoa, where they are known as *iole*. It would be interesting to obtain material for comparison, from all of the high islands of Polynesia.

Unlike New Zealand, Hawaii, the Society Islands, Tuamotus etc., the dog does not appear to have been present in the Marquesas in any numbers at the time of their discovery by the white man in 1595; Quiros and Alexander Dalrymple, however, record the theft of a bitch at that time. The naturalist, Johan Forster (1778), who accompanied Captain Cook in 1774, states that the natives of the Society Islands then possessed *both* the hog and the dog, but that the Marquesans had only the former. An effort is being made to assemble the various descriptions of this aboriginal dog, known to the Maoris as *kuri*, the Tongans as *kuli*, the Samoans as *uli*, the Rarotongans as *kuri*, the Hawaiians as *ilio*, the Tahitians as *uri*, the Tuamotuans as *kuri*, the Mangarevans as *kuri*, and the Marquesans as *nuhc*, but now extinct, with a view to reconstructing a composite picture, and ascertaining its supposed status taxonomically.

ENDEMISM

As Mr. Adamson and I have stated elsewhere (Mumford and Adamson, '33) island endemism is developed in the Marquesas to a remarkable degree. Mohotani and Fatuuku alone appear to have few, if any, species peculiar to them. The Marquesas, like the Hawaiian and Society Islands, lie roughly in a chain stretching from northwest to southeast, but it is still too early to sum up the biological evidence regarding the relative habitable ages of different parts of the chain, and to compare the Marquesas in this respect with the Hawaiian and Society Islands, where there is some evidence of an increase from south to north in the ages of the islands.

ORIGIN AND AFFINITIES

Regarding the origin of the Marquesan fauna, all that I am prepared to say at the moment is that most of it probably came from the south-west, but that there are traces of possible secondary affinities with Hawaii, the Americas, and perhaps elsewhere.

I am also still unwilling to express an opinion on the vexed question of past land connections in the Pacific. As stated in our previous paper, the almost complete absence of coral reefs from the Marquesas was attributed by Dana ('72) to rapid subsidence, and Brown ('24) has expressed the opinion that the Marquesas were once from three to six thousand feet higher than at present. Lawrence Chubb ('30) postulates alternating elevation and subsidence. A critical consideration of the evidence advanced by these scientists cannot be undertaken here. It is, however, safe again to state that the degree of island endemism shows that the individual islands in the Marquesas have been separated over a long period. Any decision on possible connections between the islands in the very remote past should, as we have already said, be based on a consideration of the fauna and flora *as a whole* and, perhaps, to be of much value, would require a better understanding of the problems of dispersal, establishment, and evolution than has been reached up to the present. In any case such decisions are always open to question, unless supported by evidence in the field of geology. Certain groups, like the flat-worms, land-snails and atyid decapods, seem to favor the "continental" hypothesis, while others would seem to support the "oceanic" theory.

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THE SPAWNING OF THE SILVER SMELT, *HYPOMESUS PRETIOSUS*

W. F. THOMPSON AND ASSOCIATES¹

University of Washington

The breaking surf of our outer seacoasts creates a zone of shifting sand and gravel of great interest to the zoologist. The animals found there must adapt themselves to constant changes which in one sense are complex yet in another are simple and direct physical consequences of wave action and of the tidal ebb and flow. Of these animals, the grunion (*Leuresthes*), the Pismo Clam (*Tivela*), Razor Clam (*Siliqua*), and Sand Crab (*Emerita*) have been studied in California beaches, each of them showing beautiful adaptations to their particular habitat.

One of the fishes taken on beaches south of Santa Barbara, California, is a small smelt-like Atherinoid, *Leuresthes tenuis*, the Grunion, which takes advantage of the shifting sand to deposit its eggs high on the beach where they remain to be liberated at the proper time by the tides. The studies by Thompson ('19) and Clark ('25) have shown that the inshore migration and the spawning habits correspond with marvelous exactness in time and character to the tidal cycles as they affect the beach. The observations recorded in this paper were inspired by these studies and describe another adaptation of this kind, differing in an interesting way.

The basic physical phenomenon to which the Grunion is adapted is a simple one. The breaking wave, dissolving in a mass of foaming water that floods the beach above, picks up and carries with it much sand and fine gravel from the part of the beach on which the break occurs. The upward rush of water has momentum and speed enough to carry its burden of sand, perhaps even adding to it, until it reaches nearly its maximum height on the slope, carrying the lighter particles farthest. As the mixture of sand and water slows, pauses for a moment, and reverses direction, the sand drops, and the water either sinks into the porous beach or drains away in a sheet that quickly gains momentum. It does not, however, have sufficient power to again pick up the sand until some two or three feet down the beach, where, moreover, the sand has been already softened and lightened by the water. The result is that the area of beach touched by the lip of the breaking wave retains and adds to its sand, but that below is eroded. For every wave that breaks on a

¹ F. H. Bell, H. A. Dunlop, L. P. Schultz, and R. Van Cleve. The observations recorded herein, both in the field and laboratory, were made jointly by all five authors during the summer of 1932, as a contribution from the Department of Fisheries of the University of Washington.

beach of uniformly textured sand there is hence very definitely what may be termed an *area of deposition*, and at a lower level an *area of erosion*. To these and the shift in position of these two areas up and down as the tides change, many beach dwelling animals adapt their habits and their structure.

On a beach containing a mixture of sand and fine gravel the areas are less sharply defined but are present nevertheless. And on a beach of coarse sand the slope is much steeper than on a beach of fine sand because of the difference in the distance which the water can carry a burden. In other words, the areas of erosion and deposition are closer together, contrasting more sharply. They are more irregular, so that the eggs are less secure, which is perhaps one reason why beaches of finer sand are seemingly more suitable for such animals as the Grunion and Pismo Clam.

The small smelt-like Grunion, burrowing tail foremost in the loosened sand, buries its eggs at the lower edge of the area of deposition, and hence along the upper edge of the area of erosion, so that the pod of eggs is more deeply covered and protected by deposition of sand as the tide falls and brings the area of deposition down the beach. The fish spawn only during and shortly after the highest part of the tide, and were it to do otherwise, for instance on the incoming tide, the area of erosion would necessarily rise on the beach and dig up the buried eggs, undoing the act of protection. But a further danger exists, for the tides on subsequent nights rise successively higher and then fall in series. Spawning takes place only after the highest of the tides in a series, otherwise the area of erosion on the night following would rise farther on the beach and do what the incoming tide of the bridal night might have done, dislodge the carefully laid eggs.

But the period of development of these eggs, left high on the beach by the outgoing tides of one series, is adapted to the time that elapses before the next series reaches them. After two weeks of lower tides, the crest of another series sweeps the area of erosion up the beach to and beyond the waiting pods of eggs, to dig them up. They hatch as they are freed from their imprisoning sand, and the larvae swim or are carried out through the surf to the open sea. And of course, since there is but the season from March to July during which such series of tides properly alternate, the season of spawning corresponds to these external events. The Grunion, making use of the area of sand deposition in each wave, has come by internal adaptation to fit its spawning habits and its reproductive rhythm, as one may call the periodic development and ripening of its eggs and milt: first, to the highest waves that reach farthest; second, to the time during the tide when it has just turned; third, to those days when the tidal series have reached their crests and are declining; and fourth, to the proper season of the year. Its spawning times, totaling but an hour or two for each of six nights in a month, fit with exact precision into the ordered sequence of the tides.

Since realizing this fascinating series of adaptations, the senior author has observed with interest the effect on many animals of the shifting sands

of our western beaches. The beaches are frequently turned over by each tide to a depth of a foot or more as the area of erosion sweeps up and down, only to have a new layer, sometimes three, sometimes six inches in depth, deposited over the surface. Such animals as the clams, of which there are two important species, the Pismo and Razor (*Tivela stultorum* and *Siliqua patula* Dixon) on the finer sand beaches, live by virtue of their adaptation to this shifting medium. The Pismo has an extremely heavy shell and burrows, thus keeping itself safe from the waves which might dig it out. It strains its food from the sand-filled water by means of a filtering screen across its inhalent siphon. The Razor Clam travels rapidly through the sand, by virtue of its shape and large foot, and keeps, when necessary, to depths too great for injury by the area of erosion. The small Sand Crab (*Emerita*) scurries down the beach at intervals as the tide falls, to bury itself anew in the soft sand below the area of deposition, where it strains from the drifting sand and water the sand-dwelling diatoms, etc., on which it feeds. Of fishes, the coasts of Washington and Oregon possess two species which are taken in quantity in the surf, the silver or day smelt (*Hypomesus pretiosus*), and the night smelt (*Spirinchus starksi*). But in none of these cases except that of the Grunion has the mechanism of adaptation to wave action received much attention.² Weymouth ('23) and Weymouth and McMillin ('31) have described the structure and growth of the two clams mentioned.

It was therefore with much interest that the senior author received a request from various people in the town of Yachats, Oregon, regarding the importance of a certain type of fine gravel, or rather very coarse sand, to the spawning run of the Smelt (*Hypomesus*). Bottles of this gravel, with samples of the ripe fish, were forwarded. It appeared that in the course of road building, quantities of this gravel were being taken from the particular beach, where the local inhabitants and tourists were accustomed to find Smelt

²In view of the spawning habits of the Grunion and Silver Smelt, much interest attaches to accounts of the spawning of the Capelin (*Mallotus villosus* Müller). The eggs of this species are adhesive and are laid "on sandy bottom along shore from just below tide mark down to 35 or 40 fathoms, where they stick together in clusters like herring eggs" (Bigelow and Welsh, '25, p. 142). (See also Fraser, '16, p. 20.) Lanman ('74, p. 225) says: "The manner in which the capelin deposits its spawn is one of the most curious circumstances attending its natural history. The male fishes are somewhat larger than the female, and are provided with a sort of ridge projecting on each side of their back-bones, similar to the eaves of a house, in which the female capelin is deficient. The latter, on approaching the beach to deposit its spawn, is attended by two male fishes, who huddle the female between them, until the whole body is concealed under the projecting ridges, and her head only is visible. In this position all three run together, with great swiftness, upon the sands, when the males, by some inherent imperceptible power, compress the body of the female, between their own, so as to expel the spawn from the orifice and the tail. Having thus accomplished its delivery, the three capelins separate, and paddling with their whole force through the shallow water of the beach, generally succeed in regaining once more the bosom of the deep; although many fail to do so, and are cast upon the shore, especially if the surf be at all heavy."

in sufficient quantity to prove of great attraction to tourists. The making of the request was significant of two things; one, that some connection between this gravel and the act of spawning was surmised, the other that the spawning run was confined to a relatively small area of beach. The gravel was so different in texture and size of grain from the fine sand in which the Grunion spawned that it naturally aroused much curiosity, as indicating different spawning habits.

The only account in the literature is that of Swan ('81). He observed the spawning of the Silver Smelt in a cove near the mouth of the "Quillehute" River, a small stream thirty miles south of Cape Flattery, where the "Quillehute" Indians collected and dried them for food, but he made no detailed observations as to spawning habits.

He speaks of them (p. 43) as "... a very choice variety of smelt (*Hypomesus olidus*), which I have named the surf-smelt, from its peculiar habit of depositing its spawn among the shingle of the beach, coming in with the surf in incredible numbers, and in this respect somewhat resembling the capelin (*Mallotus villosus*) of New Brunswick."

Again he says (p. 44): "The surf-smelt are usually most plentiful during the month of August, and come in such vast numbers that the water seems to be filled with them."

"The smelts come in with the flood tide, and when a wave breaks on the beach they crowd up into the very foam, and as the surf recedes many will be seen flapping on the sand and shingle, but invariably returning with the undertow to deeper water."

Regarding the manner of spawning (p. 45): "An examination showed the pebbles to be encrusted with spawn, and as all smelts I cooked were males, I concluded that the females had first come and cast their spawn and were succeeded by the males, who deposited their milt. I handled and noticed a great many, and cooked several dozen on two successive days, but did not notice a single female. This might have been purely accidental, and perhaps at another time the catch would have proved all females."

And finally (p. 46) as a postscript to his report: "I omitted to mention that the surf-smelt are common in all the salt water of Puget Sound, but I have not heard of an instance where they run up fresh-water streams to spawn, like the eastern smelt."

The authors found that the Silver Smelt was at the time spawning on the outer coast of the Olympic peninsula, Washington, and on August 12, 1932, they visited the beaches in the vicinity of Cedar Creek (47° 43' N., 124° 25' W.) some distance north of Aberdeen by road. There had been a run the preceding day at 4:30 P.M., and the fishermen were awaiting another at 5:30 P.M. on the rising tide, but none came. On the following day at 10:45 A.M., a good run appeared and continued until nearly 2:00 P.M., during a falling tide. On August 15, the Smelt began to spawn about 11:00 A.M., continuing until the middle of the afternoon. Again on the same day, between 5:00 and

7:30 P.M., a good run occurred, but no fishermen were present. The following day the Smelt fishermen expected a run on the incoming morning tide, but none appeared.

The coast in this region is open and broken, with short irregular beaches on which the surf beats heavily between the rocky reefs and cliffs, so that the sand and gravel on which spawning occurred was of relatively small extent. The particular beach in question was completely exposed by an extreme low tide, being bordered to seaward by sunken reefs of flat bare rocks. A small stream flowed out at its north end, adjacent to the area in which the heaviest spawning occurred. The fine gravel and coarse sand, over which the fish were spawning, extended downward about 25 yards from high tide mark and along the beach for about one hundred yards to where the sand was finer and the gravel lacking.

The fish appeared in the curling crest of each wave as it broke and were caught by a square-ended dip net thrust underneath the breaking crest. The sexes were easily distinguished. The males were smaller on the average and with a distinct golden yellow tinge, especially ventrally, while the females were of a clean silvery white. Milt and roe were readily expressed from the great majority of the fish taken. The proportions of the sexes in the sample taken and their lengths may be seen in the following table, showing that Swan ('81) was incorrect in supposing that there was a segregation of sexes.

TABLE I. *Length-frequencies of males and females of Hypomesus pretiosus, taken at Cedar Creek, August 13, 1932*

Length in mm.	Frequency	
	Male	Female
125-129.....		1
130-134.....	3	2
135-139.....	12	1
140-144.....	16	6
145-149.....	13	3
150-154.....	6	4
155-159.....	18	5
160-164.....	16	4
165-169.....	6	8
170-174.....	1	6
175-180.....		8
Total number.....	91	48
Per cent of total.....	65.5	34.5
Average length mm.....	151.3	159.8

As the wave broke and the momentum carried a sheet of water, perhaps on the average six inches deep, up the beach, the fish could be felt as they struck one's boots, and indistinctly seen as they swam rapidly to and fro through the sand and air-bubble laden water. Among the five observers present, it was the consensus of opinion that a female was accompanied by

one to three or four males, which swam parallel to and slightly behind the former. The males swam pressed against the sides of the female, and—according to one of us—so tilted that their vents were close to that of the female. The female did not bury itself but swam so low that eggs deposited at that instant would be well mixed with the water-lightened sand and gravel then settling and rolling along the bottom. It was impossible to observe the expression of eggs, but conceivably they were temporarily buried in the water-lightened gravel. The fish made no attempt to enter the area of deposition in which the Grunion lays its eggs, but remained lower on the beach within the zone of rapidly running water, and could be seen actively paired during the brief interval when the wave had paused in its upward course and was beginning its downward flow. At that instant the clouded water showed some tendency to clear, and observations were more readily made. This indicates that the eggs were laid among the cleaner larger grained coarse sand or fine gravel which had at that instant temporarily settled, the coarser material first, while the finer sand particles were still afloat. The eggs were, perhaps, granted a moment's rest in this momentarily deposited fine gravel before the wash of the next wave.

Nets were used to catch the mating fish, and for this purpose were held against the receding wave. The web became covered with small masses of eggs, adhering to the particles of fine gravel and sand. It was apparent that during the momentary rest in contact with the settling gravel, the newly extruded eggs had attached themselves by some viscous secretion which had rapidly hardened in the water. When eggs were taken from a female and fertilized, they also adhered at once to the bottom and walls of the container used. It was apparent that we were dealing with one of the many adaptations for attaching eggs to objects, and the pedestals upon which the eggs of other smelts are found were immediately brought to mind. In this case, however, the eggs were, by attachment to grains of rock, acquiring small *anchors* to hold themselves secure against being washed out to sea.

This being true, the whole sequence of events is plain. The spawning was so done that the eggs were laid while the larger particles of sand and gravel, dropping to the bottom first, were more or less concentrated and clean and of proper size for use as anchors. The finer particles, unsuited for anchorage, were in suspension or being deposited by the upper lip of the wave in the area of deposition of which the Grunion makes use. The action of the waves, in thus sorting the gravel and sand, was as definite a phenomenon as that which the Grunion (see above) makes use of, and the Silver Smelt spawning was as clearly correlated with this action of the waves as that of the Grunion with the tidal ebb and flow.

To corroborate this distribution of the particles of sand, a series of samples of sand and gravel was taken along a line from a point above high water to one beyond the break of the waves. Only the surface was used. The following table illustrates the change in size of particles in sixteen such samples

taken about three feet apart. The waves had left, at the furthest inshore levels, a surface layer of fine sand, small enough to pass through a mesh of 14 to the inch. This fine sand predominated through the area of deposition, becoming displaced by coarser as the deposition was displaced by erosion, until finally in the swifter flowing more turbulent water, the coarser grains, many of them small pebbles which would not pass through a mesh of 3 to the inch, predominated.

In the sixteen samples taken, the gravel and sand were separated into sizes by means of a Tyler Standard Screen Scale, such as is usually used by mining engineers and geologists. Screens of 3, 6, 10, and 14 meshes to the inch were chosen, and in the accompanying table the sizes thus separated are indicated by *A* for sizes that did not pass through a screen 3 meshes to the inch, *B* for those passed by 3 and held by 6, *C* for those between 6 and 10, *D* for those between 10 and 14, and *E* for those passed by 14. The weight in grams of each such size in each sample is shown in table II as the percentage this weight is of the total sample.

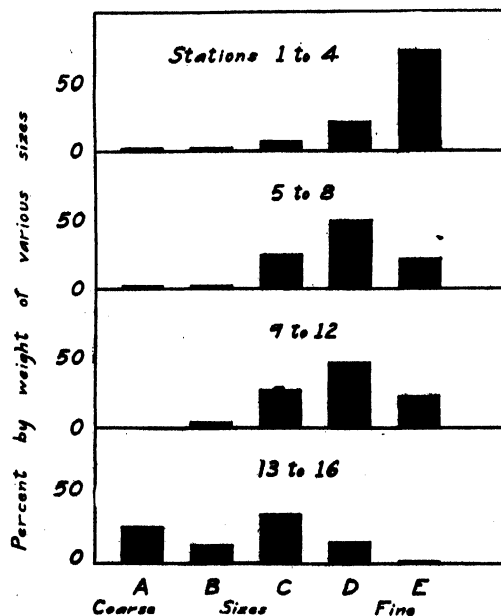


FIG 1. Percentage by weight of the various sizes of sand and gravel, taken at different stations on the beach at Cedar Creek, August 13, 1932.

For graphical presentation in figure 1 the stations are combined by fours, and the percentage each size is of the total weight of the sample is shown by the height of the bars. Size *E*, the finest sand, is abundant inshore and almost lacking in samples 13 to 16. Size *D* is at a maximum half way down the beach (stations 5 to 12), where the wash of the waves was pronounced. *C* became considerable at a still lower level and was most abundant at the outermost station.

TABLE II. *Sizes of sand and gravel given as percentages which each size formed by weight of the sample from each station in a section across beach from above to below tideline. Compared with a sample to which eggs were attached*

Stations	Percentage of Sample passed by mesh				
	A	B	C	D	E
1.....	3	3	5	6	83
2.....		1	1	5	93
3.....			7	30	63
4.....		+	11	40	49
5.....		+	12	45	42
6.....		1	25	54	20
7.....		+	37	53	9
8.....	2	2	26	49	21
9.....			16	53	31
10.....		1	18	52	29
11.....		2	28	47	23
12.....		10	45	35	10
13.....	14	11	41	28	5
14.....	21	12	39	24	5
15.....	20	19	45	14	2
16.....	54	16	22	7	1
Sample with eggs.....		11	43	26	20

For comparison, a typical sample of gravel with eggs attached showed:

Size B	11	per	cent
" C	43	"	"
" D	26	"	"
" E	20	"	"

which corresponds approximately to sample 12 of table II, hence in the section of the beach washed by the stronger currents.

We found that the layers of sand in vertical sections of the beach, as they were left in succession by an earlier ebbing tide with the area of deposition of fine sand last, corresponded to this surface distribution of particles. Samples were taken at six different levels, from the surface down ten inches. It was expected that the deeper levels would be those reached by the stronger currents of the last eroding area, hence filled with larger particles which would be buried by deposition, first of gravel, then of sand as the tide ebbed, while the final surface would be formed by the area of deposition of fine sand, the last to pass over the beach with the falling tide. As will be seen (fig. 2), our series of samples corresponds nicely to this expectation. The surface corresponds to the finer sand of the most shoreward samples of the preceding series, the lowermost of the vertical samples to the coarse gravel of the outermost samples taken in the wash of the waves.

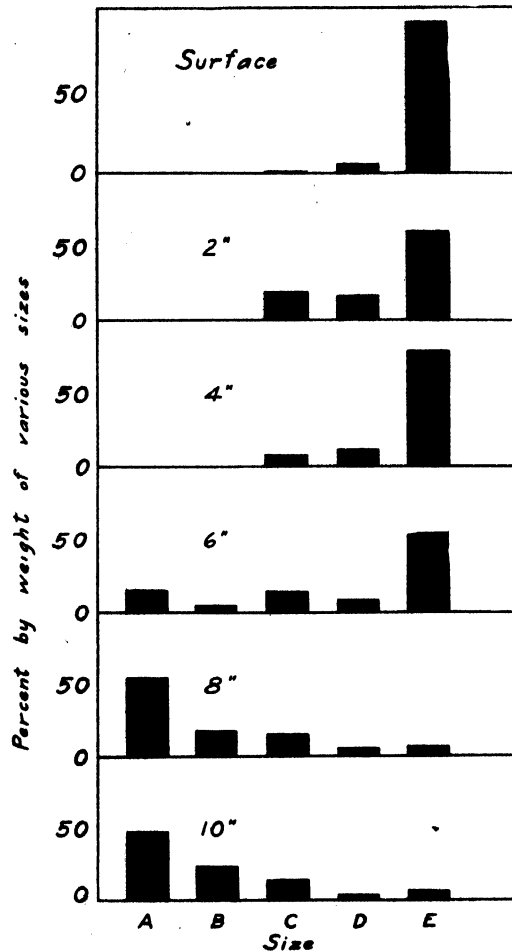


FIG. 2. Percentage by weight of each size of sand and gravel in each of six samples taken vertically at two inch intervals, on the beach at Cedar Creek, August 13, 1932.

TABLE III. Sizes of sand and gravel given as percentages which each size formed by weight of six samples taken vertically at two inch intervals at one point on the beach

Sample	Size of Mesh				
	A	B	C	D	E
1			1	6	93
2			20	17	63
3			8	12	79
4	17	5	14	8	56
5	55	19	16	4	6
6	49	25	16	4	6

The Silver Smelt is therefore plainly adapted to the surf phenomenon put to such precise use by the Grunion. But where the Grunion, spawning on fine sand beaches at sharply limited times, uses but one particular part of the

wave-swept zone, that at the lower edge of the area of deposition, the Silver Smelt frequents those beaches on which the waves expose proper sized anchors of fine gravel, and this use of the wash of the waves is primarily to give access to the cleaned gravel of right size. It seems to spawn whenever this is possible, although it also has in so doing added advantage in the fact that as the tide recedes the upper edge of the wash deposits over this a layer of fine sand which protects the eggs to some extent and holds the moisture.

Its eggs, once anchored properly, can stand repeated washings, the capsules being firm and strong. The egg-covered gravel was found from extreme low tide level, where the bare rocks were exposed, to a point more than half way up the beach, and to depths of a foot or even more. It must have been worked and turned over by every tide. The pounding of the surf is, perhaps, not so violent in its effects as it appears, since fairly delicate organisms can survive it unless thrown against or caught between rocks and boulders, but the strength of these eggs was such as to suggest that they could survive the ordinary pressure of the observer's foot on the sand.

There is, however, a fact in this connection which may bear further examination. The Smelt is known to run only during the day from May to September. When one examines the tide tables, it is seen that during this period the day tides are lower than the night tides. Were the spawning to occur at night, the eggs would, at least on the higher levels, be left for nearly twenty hours in the drained sand, exposed to sun and rain. But spawned during the day, as they are, the eggs are washed by the night tide less than twelve hours later, and the beach in which they are laid is never as dry as it becomes at higher levels. This is a possible relationship of much interest, analogous to the adaptations of the Grunion to the time of the tidal series.

We have observed the same species of Smelt spawning on beaches in Puget Sound where the wave action is very much less than on the outer coast. The eggs are laid on the beach in coarse sand or gravel as in the ocean form. But our observations have been neither thorough nor frequent enough to justify any comment on our part as to what happens there. Some possibility exists that the Smelt in Puget Sound is a different race from that on the ocean beaches.

The other smelt taken on the ocean beaches, called Night Smelt, has not been observed spawning by us. But it is not likely that its eggs were laid attached to the same sized fine gravel on the beach, because the eggs taken on the sand during the spawning of *Hypomesus* are homogeneous in size, and they are similar in appearance to those taken from the female Silver Smelt for artificial fertilization. The eggs vary from 1.00 to 1.12 mm. in diameter.

Only preliminary egg counts have been made due to the fact that extensive study of the life history of the species is necessary before a proper estimate of the egg production may be achieved. The following counts, taken from specimens in which apparently there had been no recent extrusion of eggs, provide an approximation to the number of developed eggs in the ovary at

the time of spawning. These counts include only the mature eggs, there being several sizes of eggs that apparently were being proliferated at the anterior end of the ovary.

Length of fish in cm.	Egg count
15.0	4020
15.5	7260
15.9	8880
16.5	7980
16.9	13714

Arrangement of these few individuals by length may be taken to indicate an egg production increasing with size.

The eggs develop with a rapidity comparable to that of the Grunion. Some of those taken on the 13th and killed on the 17th had the form of the embryo well developed and pigment in the eyes. It was of course not known when these had been laid, but it was fair to conclude that development to and beyond the eyed stage took place in gravel exposed to the waves.

In the case of the Silver Smelt, as in that of the Grunion, there is seen again what it is fair to term exquisite precision in adaptation of habit to physical phenomena on the beach. We may conclude that in both, existence depends upon a fundamental order in the seemingly casual shifting of the sand on the beaches.

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REVIEWS

LIMNOLOGY ¹

This book is the outgrowth of a general introductory course in limnology that has been given by the author for a number of years. The material is well chosen for such a course and it consists largely of results that have been obtained on American lakes and streams.

The geological phase of limnology deals with the origin of lake basins, the dynamic action of the water on the shores, the size, depth and elevation of lakes. The discussion of the physics of lakes includes the annual temperature changes, thermal stratification, heat budgets, and the penetration of solar radiation into various types of lake waters; the absorption of solar energy by colored lake waters is well illustrated.

Water is an excellent solvent so that a wide variety of substances is found in solution; these solutes include dissolved gases, silica, phosphates, nitrates, calcium, magnesium, iron and various other inorganic constituents. Organic materials are found also, either in a particulate form or in true solution.

The ecology of fresh water is especially emphasized in chapters VI and VII which contain a discussion of the relation of the physical and chemical conditions of the water to the biota. The responses of plants and animals to these factors are shown by changes in form, by photosynthesis, by streamlining, by migrations, by changes in metabolic rate and by various other adaptations to the physical and chemical conditions found in lake waters.

The constituents of the plankton are discussed, as well as their geographical, horizontal and vertical distribution and the factors which determine these phenomena. The plankton production of a body of water is discussed and the physical, chemical and biological agents which affect it. The chemical composition of the plankton is included also. The microscopic and the large aquatic plants constitute the fundamental food of the aquatic animals and thus play a most important rôle in lake economy. The benthic regions are classified, and the quality and quantity of benthic life are discussed. A discussion of the circulation of the food materials is given also and a classification of lakes on the basis of their productivity is presented.

The last three chapters are devoted to the consideration of special types of water, such as ponds, bog lakes and streams. These are followed by a good classified bibliography covering 54 pages.

C. JUDAY

UNIVERSITY OF WISCONSIN

¹ **Welch, Paul S.** 1935. *Limnology*. xiv + 471 pp. *McGraw-Hill Book Company*. New York. \$5.00.

ZOOPLANKTON¹

In the preface of this book, the author states that it is intended as an orienting introduction to the systematics and the ecology of the animal constituents of the limnoplankton. In the first chapter the term plankton is defined and definitions are also given for the various types of plankton; in addition, it includes a discussion of the adaptations, temporal variations and distribution of the zooplankton constituents.

The following five chapters deal with the taxonomy, the ecology and the seasonal form variations of the protozoa, the rotifers, the cladocera, the free living copepods and the other animals belonging to the limnoplankton such as *Mysis* and insect larvae. Identification keys and descriptions of the various species are given and thirty plates of line drawings also assist one in the identifications. Only the more common constituents of the zooplankton of European lakes are represented in the different groups; a brief ecological summary is given for each group. A list of synonyms is given at the end of the book and this is followed by a bibliography of 37 pages.

C. JUDAY

UNIVERSITY OF WISCONSIN

A MARINE ESTUARY¹

This fairly comprehensive ecological study of a marine estuary opening into Monterey Bay, California, describes the various physical and biotic factors together with the relations of the animals to these factors and to each other. The bulk of the paper deals with a catalog of the animals with notes on their natural history. The fauna is definitely marine, no invading fresh water forms occurring in this particular situation. A series of photographs illustrate the region and some of the characteristic animals.

A. E. EMERSON

UNIVERSITY OF CHICAGO

THE ORIGIN OF MAIZE

The phylogeny of maize has interested botanists and archaeologists of the Americas for over a quarter of a century. In introducing the subject Weatherwax¹ shows that it is very difficult to determine the ancestry of a domesticated plant such as maize by direct methods. Indian traditions are held to be valueless and what meager records there are date back less than 500 years. Although Mayan exploration promises some light on the origin

¹ Rylov, W. M. 1935. Das Zooplankton der Binnengewässer. Bd. XV, Thienemann's Binnengewässer. ix + 272 pp. 15 figs., 30 pl. Stuttgart. RM. 30.00.

¹ MacGinitie, G. E. 1935. Ecological aspects of a California marine estuary. *Amer. Midland Nat.* 16 (5): 629-765.

¹ Weatherwax, Paul. 1935. Phylogeny of *Zea mays*. *Amer. Midl. Naturalist* 16; 1-71.

of the maize, it has revealed little of value to date. Thus the author turns to the plant itself in an attempt to extract from it, by indirect methods, its own life story.

The author then takes up in order its taxonomic position, vegetative anatomy, cytology, inflorescences, structure of the ear, and theories as to the origin of the ear. *Zea mays* belongs to the American group of the tribe Maydeae which includes *Tripsacum* and the *Euchlaena* (teosinte). The author points out the great similarity of the Maydeae with the Andropogoneae, especially with genera such as *Manisuris*. In both the Andropogoneae and Maydeae the primitive condition is held to be one of paired spikelets, one being sessile and the other pedicelled, each spikelet containing two florets. The present condition in the various genera is assumed to have been attained by total or partial suppression of one floret in each spikelet, and by the elimination of stamens or pistils in the remaining floret. In the Andropogoneae the flowers, or some of them, are perfect whereas in Maydeae, imperfect flowers are the rule. However, the author believes that monoecism should not be made the sole basis for forming a separate tribe. In any event, the primitive Andropogonean stock is held to have separated into two parts, the one branch leading toward monoecism (Maydeae), while the other did not. In discussing the origin of the ear he describes some studies on planed and varnished sections of cobs. He states, and supports his statements by photographs, that the members of one row are not opposite the members of adjacent rows but alternate with them. Thus a line drawn through the members of paired spikelets forms an undulating row around the axis and the problem resolves itself into a complicated problem of phyllotaxy.

Although no wild maize plants have ever been found the author describes what the wild plant must have been like and concludes that "these characteristics . . . indicate a low rate of reproduction, and we may well ask how a plant with such poor adaptations could maintain itself in nature. The answer is that it owes its preservation to its adoption by man at a critical time, and that is why wild maize is rare or extinct today." This extinction was greatly accelerated by the introduction of large grazing animals into America in the early part of the sixteenth century. Nevertheless the author thinks it still possible that wild maize may still be found in the inaccessible highland regions of Central America and southern Mexico.

In discussing the possible hybrid origin of maize the author agrees that there must have been a plant in the ancestry of maize which is now extinct or unknown. He does not feel, however, that our present maize was formed by hybridization of this plant with teosinte. Rather he believes in the direct descent of our present maize from the wild progenitor especially in view of the uncertainties connected with hybridity and the lack of sufficient evidence of hybridization. Since the nearest known relative of maize is teosinte, we might at first think that the home of wild maize should be sought in the same area. If, however, maize and teosinte arose by divergent evolution from a

common stock, there must have been some barrier between them to enable them to develop their own distinctive characters. If separated by a natural barrier they might have maintained their genetic independence in the same general region, especially in the diversified topography of Mexico and Central America. The author concludes that teosinte was originally widely distributed over the highlands and foothills of central Mexico and western Guatemala while maize was fighting a losing battle in some isolated place. Since the coming of man, however, maize has spread into every continent whereas teosinte has steadily lost ground due to the adverse influence of large herbivorous animals.

WM. T. PENFOUND

TULANE UNIVERSITY OF LOUISIANA

THE PRACTICE OF SILVICULTURE¹

After passing through a long formative period the practice of silviculture in the United States is now becoming crystallized. Knowledge concerning many phases of silvicultural practice in America is still deficient but a sufficient body of information has accumulated to permit the formulation of certain principles and methods. In "The practice of silviculture" these principles and methods are clearly set forth.

The standard reproduction methods are first considered in some detail; concrete examples illustrative of the application in specific forest types are numerous. In this and subsequent sections one finds a large amount of information on the ecological characteristics of the more important forest trees. Three chapters are devoted to intermediate cuttings. It is the reviewer's opinion that Hawley has succeeded in presenting the clearest and most concise discussion of this phase of silviculture that is available in American writings. One chapter each is devoted to methods of controlling cuttings and slash disposal. Nine chapters are devoted to protection of the forest against agencies such as fire, insects, diseases, domestic animals, wild animals and natural phenomena.

Although writing with particular reference to the application of silviculture in the United States, Hawley has not ignored or minimized European experience. Far from it. The more important foreign contributions have been given due consideration.

At the end of each chapter is a carefully selected and accurately cited list of references to American and foreign literature. This feature adds considerably to the reference value of the book. The clear, concise, and authoritative character of "The practice of silviculture" will be appreciated by every ecologist who is interested in forest communities.

H. J. LUTZ

YALE UNIVERSITY, NEW HAVEN, CONN.

¹ Hawley, Ralph C. 1935. The practice of silviculture with particular reference to its application in the United States of America. Third edition, rewritten and reset. pp. xv + 340. 68 figs. John Wiley and Sons, Inc., New York. Price \$4.00.

ADVANCING DESERTS

Scientists have long been aware of the destructive use of land by American pioneer farmers, ranchmen, and lumbermen, but it is only within past decade that the public has come to appreciate the same fact. The recent years of drought have helped to make the American farmer erosion conscious but the general public still has little appreciation of the immense scale upon which these destructive agencies are operating. Education is necessary and the articles on erosion and erosion control are numerous. Two recent contributions should be of special interest to ecologists.

Sears¹ with a keen sense of the dramatic has drawn a picture of the conditions in other lands as well as in our own. He conceives of the soil, exhausted by man, rapidly becoming defenseless against flood, drought, and wind until it rises in great clouds that hurl themselves against the homes and cities of the destroyer. Across our continent he traces white destructive culture as it moves westward by different routes to the regions of the grassland. Here, with the turf broken by grazing herds and by the plow of the farmer, the drought and the winds raise a dust storm of protest that hurls the desert eastward over the plains.

Thus in non-technical terms the ecological problems of the desert, grassland, and forest are discussed, water is shown to control the pattern of vegetation for the continent as well as that of land utilization. If this utilization is to be effective the lesson of conservation must be learned, in order that resources may be used rather than destroyed. Such a statement should tend to rouse the reading public to a knowledge of ecological truths so that the progress of advancing deserts may be checked.

The second of these articles comes from an observer from another land that has suffered even more severely than our own. Gorrie,² of the Forest Service of British India, spent a considerable portion of 1934 in the United States and reports the results of his observations. Among other things he cites the results of accelerated soil erosion caused by over grazing and by the devastation of forests, especially in semiarid regions. Attention is directed to the loss of soil due to bad farming and to attempts to cultivate areas of rather dry grasslands with the result that it is estimated that over 300 million tons of organic material are annually lost from the soils of the United States; a loss of 50 to 60 tons of soil per acre has been verified in certain types of wheat and maize cultivation. In arid regions where irrigation has been attempted the reservoirs are silting up and losing their storage capacity at a rate of over one per cent per annum.

These and other similar data presented in a thoughtful manner make the report worthy of careful consideration.

THE UNIVERSITY OF CHICAGO.

GEO. D. FULLER

¹ **Sears, Paul B.** 1935. *Deserts on the March*. 231 pp. *University of Oklahoma Press, Norman, Oklahoma*. \$2.50.

² **Gorrie, R. MacLagan.** 1935. *The use and misuse of land*. *Oxford Forestry Memoirs, No. 19*. 80 pp. 5 pl. *Oxford University Press, N. Y.* \$2.00.

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SURVEY OF FOREST RESEARCH PROJECTS

The Committee on Forestry of the National Research Council has undertaken a survey of Forest Research projects being conducted within the United States for the purpose of determining neglected fields, indicating projects worthy of additional support, and of acquainting the profession generally with the scope of work now under way.

Through regional secretaries, the committee has endeavored to reach all institutions and individuals having research work under way which has a bearing on forest practice. It is requested that any individuals or agencies having projects which should be included and that have not been contacted by regional secretaries get in touch with the Secretary of the Committee.

HARDY L. SHIRLEY,
University Farm, St. Paul, Minn.
Secretary Committee on Forestry

NOTES AND COMMENT

SURVIVAL VALUE OF AGGREGATIONAL BEHAVIOR OF BASS UNDER ADVERSE CONDITIONS

In the March, 1916, N. Y. Zoological Society Bulletin, Dr. C. H. Townsend made the following comments on page 1345:

"When winter weather comes and the temperature of the fresh water, flowing through the tanks of the Aquarium falls below forty degrees, Fahrenheit, some of the fresh water fishes become very sluggish.

"Young black bass are affected by the low temperature in quite a different way (from young yellow perches). They remain poised somewhere above the bottom and crowded closely together. It is a common sight to see fifty or more of them compactly bunched and all facing one way. There are two tanks of young black bass in the Aquarium, both of which exhibit this habit to good advantage while cold weather lasts."

The facts stated above are illustrated by a photograph of young small-mouth bass compactly bunched into a mass which is characterized by a vertical columnar shape. There is one column which is about seventeen fish-body-depths deep, and from three to six wide, and contains about fifty fish, while about thirty more fish form a group which is not so compact.

The behavior of yearling spotted bass, *Micropterus pseudaplites* Hubbs, in Pond No. 2 at Ohio State Fish Farm No. 12, was very similar to that described and pictured by Townsend. The temperature of the water in this pond is very uniform, and was 61° F. on the days mentioned, a point considerably higher than the "below forty" mentioned by Townsend, and the cause for this form of behavior appeared to be a factor other than low temperature.

The Spotted Bass yearlings, 1,362 in number, were placed in this pond on May 3, 1935. Most of them were then about four inches long, but a few were shorter and a few were longer than this figure. They were offered ground carp and most of them quickly formed the habit of dependence on this food supply. Their behavior was not unusual until the morning of June 10, but it continued out of the ordinary until June 14 when the pond was drained. The majority of the fish in the pond were assembled into a number (varying from 18 to 22) of vertical columns which showed as black spots at the surface of the water. These columnar aggregations were distributed throughout the pond without regard to such features as current or shade. The remainder of the bass moved in spurts around the pond, most of them close to the surface. The spurts appeared to be directed usually toward other fish, and doubling frequently resulted.

Beginning at 3 P.M. on June eleventh, some loss of fish occurred, and a total of 200 bass had died when the pond was drained. All dead fish were characterized by the complete lack of the normal coating of slime, the appearance being comparable to the results of scalding with hot water. Investigation revealed that the machinery used for taking water from the spring basin (the source of water supplying the pond) for use at the adjacent U. S. Transient Camp had become disordered in such manner that chlorine was being discharged into the spring basin. This had begun the day before the unusual aggregational behavior had been noted and was stopped when discovered on June tenth.

It appears probable that the chlorinated water caused the slime coat to disappear, and that, either because of the lack of this protective covering or because the chlorine acted also on the skin, gills, or membranes, the fish were uncomfortable. The behavior of the bass in bunching as described is certainly the result of each fish soliciting bodily contacts with other fish. This orientation of fish principally with respect to each other

rather than to other features of the environment is probably to be explained as a measure whereby the fish attained bodily comfort or overcame distress. The presence of the body of another fish in close proximity or actual contact doubtless compensated somehow for the absent slime-coat, and caused the irritation to be less acute.

One of the larger fish had swallowed a smaller one whose tail hung out its mouth. This predator maintained its position in one of the aggregations, though ordinarily the approach of a predaceous bass causes smaller bass in a group to scatter for safety.

When the addition of chlorine to the spring was stopped, the full flow of good water was turned into the pond to flush the chlorinated water out. Many of the vertical aggregations disappeared as the fish took new positions in the current though some aggregations at the end of the pond remained intact. These aggregations were presently in a weak backwash current which pushed them gently along, and in these groups all of the fish were headed in the same direction, facing in the current. In the other groups this was not the case.

The similar aggregational behavior of bass in cold water, as observed in the New York Aquarium may be explained as a case where the individuals were enabled to better meet the requirements of another adverse aspect of their environment. Cold causes a retardation in metabolic rate which may be fatal if carried beyond a certain point. Stimulating body contacts cause the opposite reaction and tend to prevent the ultimate loss of life from cold. The type of aggregations of bass described here may be considered, therefore, a manifestation of social behavior of great possible survival value for the individuals, the groups, and the species.

T. H. LANGLOIS

BUREAU OF FISH PROPAGATION,
OHIO DIVISION OF CONSERVATION,
COLUMBUS, OHIO

A NOTE ON THE SHRUBS OF A DESERT PLAINS COMMUNITY IN NOLAN COUNTY, TEXAS¹

The author had an opportunity early in August, 1934, to make a brief sampling of the vegetation on, and near, a plateau (or series of mesas) in Nolan County, Texas, which forms part of Callahan Divide, the watershed between the Colorado and Clear Fork of the Brazos Rivers. The Comanchean-topped Callahan Divide is situated in the midst of a Permian plain.

The desert plains region is a broadly rolling country broken by the occasional shallow arroyos of ephemeral streams and by infrequent mesas forming the watersheds between the larger streams. The annual precipitation is about 60 cm., little of which falls during the summer. The wind velocity is comparatively high. The soil is chestnut-brown with a calcareous subsoil.

To the casual observer, there is a monotonous similarity in the plants of the entire desert plains region, with the exception of the more mesophytic phase along water courses. The most conspicuous components of this vegetation as it now exists, are the "armed" shrubs which give the plains the appearance of desert scrub. Of these *Prosopis juliflora* DC. is the dominant shrub, with *Zizyphus*, *Opuntia engelmanni* Salm., and *Yucca* next in abundance. For the most part, there is now only a sparse herbaceous cover in this area. The samples showed that while there was considerable homogeneity of species (tables I and III), there was also much local variation (table II) in the abundance of the less numerous components.

¹ Contribution from the Botanical Laboratory of the University of Oklahoma, No. 38.

In the region sampled, the "shinnery" oaks (figs. 3 to 6) were much more abundant than over most of the adjacent desert plains, while the number of *Opuntia engelmanni* was lower. A more mesophytic community consisting largely of *Quercus texana* Buckl. (fig. 5, table II), growing in the protection of a cañon cutting into the north side of the mesa, was apparently unusual.

Four counts² were made of the shrubby components of the vegetation (table I), and percentages of occurrence were calculated and shown in table III. These were made from strips approximately a meter in width. The first two transects sampled the vegetation of the low plain, the side of the plateau, and the plateau top. The first area (tables I and II) was from a point in the low plain, south for about three kilometers to the highest point on the plateau in that vicinity. Parts of the count (table II) show considerable fluctuation due to edaphic conditions. The point of origin of the second area (table I) was the same as the first, but extended east for almost a kilometer to the center of a northward extension of the plateau. About half of each of the last two counts was from the floodplain and half on the south bank of an arroyo. The third and fourth areas were parallel, about thirty meters long, running perpendicular to an arroyo in the break of the plateau of the divide.



FIG. 1. View of the mesa top (left) showing *Opuntia davisii*, *Fagara fruticosa*, and *Prosopis juliflora*. Another view of the same area (right) showing *Opuntia leptocaulis* and *Prosopis juliflora*.

A list of the shrubs found in, and immediately adjacent to, these areas is given in tables I, II and III, which shows an interesting correlation between the counts of the shrubs of the low plain, plateau side, and plateau top.³

² The value of such counts is the ease with which they are taken and that the areas counted do not need to be accurately measured to show the percentage of composition. On the other hand, they cannot be used to compute the number of plants for a given area. Obviously the larger the counts and the more areas counted, the more accurately will the sample represent the vegetation of the region.

³ The coefficient of reliability between the counts of the low plain is $.97 \pm .009$, of the mesa side $.94 \pm .017$, and of the mesa top $.73 \pm .069$. The counts on the arroyo bank and the floodplain were so small that the coefficients of reliability are, of course, low.

TABLE I. Census of the shrubby components of the vegetation of the desert plains community in Nolan County, Texas

Species	Arroyo Bank			Floodplain			Low Plain			Plateau Side			Plateau Top			Total in all counts
	Count III	Count IV	Total	Count III	Count IV	Total	Count I	Count II	Total	Count I	Count II	Total	Count I	Count II	Total	
<i>Juniperus monosperma</i> (Engelm.) Sarg.	1	1	2	1	0	1	17	5	22	1	8	9	19	5	24	58
<i>Ephedra nevadensis</i> Watson	0	0	0	0	1	1	3	1	4	0	1	1	0	0	0	6
<i>Smilax bona-nox</i> L.	2	1	3	1	0	1	0	0	0	0	0	0	2	0	2	6
<i>Yucca</i> sp.	0	0	0	4	1	5	55	41	96	0	1	1	0	2	2	104
<i>Prosopis juliflora</i> DC. ¹	0	0	0	2	0	2	12	3	15	0	1	1	2	1	3	21
<i>Acacia urightii</i> Benth.	0	0	0	0	0	0	9	3	12	6	6	12	0	2	2	26
<i>Acacia greggii</i> Gray	0	0	0	0	0	0	1	0	1	0	0	0	0	7	7	8
<i>Acacia constricta</i> Benth.	0	0	0	0	0	0	0	0	0	0	0	0	8	0	8	8
<i>Bumelia lycioides</i> (L.) Pers.	1	2	3	5	3	8	17	14	31	0	8	8	1	1	2	52
<i>Celtis berlandieri</i> Klat.	0	0	0	0	1	1	4	0	4	0	0	0	0	0	0	3
<i>Celtis occidentalis</i> L.?	2	0	2	1	0	1	0	0	0	0	0	0	0	0	0	5
<i>Celtis georgiana</i> Small	0	0	0	1	1	2	0	0	0	0	0	0	0	0	0	3
<i>Celtis reticulata</i> Torr.	0	0	0	0	0	0	0	0	0	0	0	0	1	2	3	3
<i>Zizyphus garrayi</i> Torr.	0	0	0	0	0	0	5	1	6	0	0	0	0	0	0	6
<i>Quercus texana</i> Buckl.	0	0	0	0	0	0	0	0	0	42	0	42	0	0	0	42
<i>Quercus hypoleuca</i> Engelm.	0	0	0	0	0	0	0	0	0	6	0	6	0	0	0	6
<i>Quercus durandii</i> Buckl.?	0	0	0	0	0	0	0	0	0	10	0	10	0	0	0	10
<i>Quercus grisea</i> Lieb.?	0	0	0	0	0	0	70	77	147	140	55	195	310	24	334	676
<i>Forestiera parvifolia</i> (Gray) Small	3	1	4	1	0	1	0	0	0	0	0	0	0	0	0	5
<i>Forestiera pubescens</i> Nutt.	0	0	0	0	0	0	0	0	0	5	0	5	0	2	2	7
<i>Forestiera neo-mexicana</i> Gray	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	1
<i>Prunus rinularis</i> Scheele	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	1
<i>Lycium berlandieri</i> Dunal	0	0	0	0	0	0	1	1	2	0	0	0	0	0	0	2

TABLE I (Continued)

Species	Arroyo Bank			Floodplain			Low Plain			Plateau Side			Plateau Top			Total in all counts
	Count III	Count IV	Total	Count III	Count IV	Total	Count I	Count II	Total	Count I	Count II	Total	Count I	Count II	Total	
<i>Rhus microphylla</i> Engelm.....	0	0	0	0	0	0	4	1	5	0	0	0	0	0	0	5
<i>Rhus trilobata</i> Nutt.....	0	1	1	1	5	6	20	40	60	135	20	155	0	3	3	225
<i>Rhus leucantha</i> Jacq.....	1	0	1	2	0	2	0	0	0	0	0	0	0	0	0	3
<i>Ungnadia speciosa</i> Engl.....	0	0	0	0	0	0	0	0	0	0	1	1	1	0	1	2
<i>Clematis drummondii</i> Torr. & Gray	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	1
<i>Fagara fruticosa</i> (Gray) Small.....	1	1	2	0	0	0	0	0	0	0	0	0	1	2	3	5
<i>Opuntia filipendula</i> Engelm.?	0	0	0	1	2	3	8	5	13	0	0	0	1	2	3	19
<i>Opuntia engelmannii</i> Salm.....	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	1
<i>Opuntia leptocaulis</i> DC.....	0	0	0	0	0	0	2	0	2	0	0	0	0	0	0	2
<i>Berberis trifoliata</i> Moric.....	1	0	1	2	1	3	2	1	3	0	0	2	0	1	1	10
<i>Cephalanthus occidentalis</i> L.....	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1
<i>Baccharis salicina</i> Torr. & Gray	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	1
<i>Cercis occidentalis</i> Torr.....	1	1	2	0	1	1	0	0	0	0	0	0	0	0	0	3
<i>Lonicera albiflora</i> Torr. & Gray	0	1	1	1	0	1	1	0	1	0	0	0	0	0	0	2
<i>Ulmus americana</i> L.....	2	1	3	0	0	0	0	0	0	0	0	0	0	0	0	3
<i>Salix nigra</i> Marsh.....	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Cocculus carolinus</i> DC.....	1	1	2	0	0	0	0	0	0	0	0	0	0	0	0	2
<i>Amorpha fruticosa</i> L.....	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1
<i>Artemisia filifolia</i> Torr.....	0	0	0	0	3	3	0	0	0	0	0	0	0	0	0	3
Total.....	18	10	28	24	20	44	236	193	429	345	103	448	346	54	400	1,349

¹ Often heavily parasitized with *Phoradendron flavescens* Nutt.

In the low plain there is typically a larger variety of species than in drier situations. *Prosopis*⁴ is the most conspicuous and widespread of the shrubs. In the lowest portion

TABLE II. Census of the shrubby components of different parts of the desert plains communities in Nolan County, Texas

Species	Low plains			Plateau side		Plateau top			Total
	Part 1	Part 2	Part 3	Part 1	Part 2	Part 1	Part 2	Part 3	
<i>Juniperus monosperma</i> (Engelm.) Sarg.	15	2	0	0	1	12	0	7	37
<i>Ephedra nevadensis</i> Watson	3	0	0	0	0	0	0	0	3
<i>Smilax bona-nox</i> L.	0	0	0	0	0	2	0	0	2
<i>Yucca</i> sp.	51	4	0	0	0	0	0	0	55
<i>Prosopis juliflora</i> DC.	9	3	0	0	0	0	2	0	14
<i>Acacia wrightii</i> Benth.	9	0	6	0	0	0	0	0	15
<i>Acacia greggii</i> Gray	1	0	0	0	0	0	0	0	1
<i>Acacia constricta</i> Benth.	0	0	0	0	0	0	0	8	8
<i>Bumelia lycioides</i> (L.) Pers.	15	2	0	0	0	1	0	0	18
<i>Celtis berlandieri</i> Klat.	0	4	0	0	0	0	0	0	4
<i>Celtis reticulata</i> Torr.	0	0	0	0	0	1	0	0	1
<i>Zizyphus garryi</i> Torr.	5	0	0	0	0	0	0	0	5
<i>Quercus texana</i> Buckl.	0	0	30	12	0	0	0	0	42
<i>Quercus hypoleuca</i> Engelm.	0	0	3	3	0	0	0	0	6
<i>Quercus durandii</i> Buckl.?	0	0	10	0	0	0	0	0	10
<i>Quercus grisea</i> Lieb.?	50	90	50	80	10	59	1	250	520
<i>Foresiiera pubescens</i> Nutt.	0	0	0	0	5	0	0	0	5
<i>Foresiiera neo-mexicana</i> Gray	0	1	0	0	0	0	0	0	1
<i>Prunus rivularis</i> Scheele	0	1	0	0	0	0	0	0	1
<i>Lycium berlandieri</i> Dunal	1	0	0	0	0	0	0	0	1
<i>Rhus microphylla</i> Engelm.	4	0	0	0	0	0	0	0	4
<i>Rhus trilobata</i> Nutt.	20	0	30	60	45	0	0	0	155
<i>Ungnadia speciosa</i> Endl.	0	0	0	0	0	1	0	0	1
<i>Clematis drummondii</i> Torr. & Gray	1	0	0	0	0	0	0	0	1
<i>Fagara fruticosa</i> (Gray) Small	0	0	0	0	0	1	0	0	1
<i>Opuntia filipendula</i> Engelm.?	4	4	0	0	0	0	1	0	9
<i>Opuntia engelmanni</i> Salm	1	0	0	0	0	0	0	0	1
<i>Opuntia leptocaulis</i> DC.	2	0	0	0	0	0	0	0	2
<i>Opuntia davisii</i> Engelm.	1	0	0	0	0	0	0	0	1
<i>Berberis trifoliata</i> Moric.	2	0	0	0	0	0	0	0	2
<i>Lonicera albiflora</i> Torr. & Gray	1	0	0	0	0	0	0	0	1
Total	195	41	129	155	61	77	4	265	927

of the low plains *Acacia*, thickets of *Bumelia*, *Rhus microphylla*, *Rhus trilobata*, *Opuntia* spp., and an occasional *Lycium*, *Berberis*, and *Lonicera* are found with the *Prosopis*. Just above this there is a zone of *Prosopis*, *Zizyphus*, *Clematis*, and *Ephedra*, which is replaced in the (east and west) approaches to the plateau by *Yucca*, *Opuntia*, *Juniperus*, and *Quercus grisea* Lieb (?), while the stand of *Prosopis* is very sparse (figs. 3 to 6).

On the west side of the plateau "shinnery" (*Quercus grisea* Lieb.?) is the most abundant component (fig. 4). There is also a good representation of *Acacia*, *Bumelia*,

⁴ It is to be noted that these counts do not evaluate the size of the components, so that, for example, one *Prosopis juliflora* will be far more conspicuous than many *Quercus grisea*.

and *Juniperus*. On the north side of the plateau, at the base, is a community of *Quercus texana* Buckl. (fig. 5), while near the rim are found several plants of *Forestiera*.

Near the rim of the plateau, and on much of the high plains of the plateau, juniper and shinners are the most conspicuous shrubs although much of the high plains is an *Aristida* community with a scattering of *Juniperus* and *Prosopis* (fig. 1).

TABLE III. Percentage frequency in the occurrence of the components of the desert plains community enumerated in table I

Species	Ar-royo bank	Flood plain	Low plain	Plat- eau side	Plat- eau top	Total
<i>Juniperus monosperma</i> (Engelm.) Sarg.	7.1	2.4	5.1	1.9	6.0	4.35
<i>Ephedra nevadensis</i> Watson	0.0	2.4	0.9	0.2	0.0	.45
<i>Smilax bona-nox</i> L.	10.7	2.4	0.0	0.0	0.5	.45
<i>Yucca</i> sp.	0.0	12.1	22.7	0.2	0.5	7.80
<i>Prosopis juliflora</i> DC.	0.0	4.8	3.4	0.2	0.7	1.57
<i>Acacia wrightii</i> Benth	0.0	0.0	2.8	2.6	0.5	1.95
<i>Acacia greggii</i> Gray	0.0	0.0	0.2	0.0	1.5	.60
<i>Acacia constricta</i> Benth.	0.0	0.0	0.0	0.0	2.0	.60
<i>Bumelia lycioides</i> (L.) Pers.	10.7	19.4	7.2	1.7	0.2	3.82
<i>Celtis berlandieri</i> Klat	0.0	2.4	0.9	0.0	0.0	.37
<i>Celtis occidentalis</i> L.?	7.1	2.4	0.0	0.0	0.0	.22
<i>Celtis georgiana</i> Small	0.0	4.8	0.0	0.0	0.0	.15
<i>Celtis reticulata</i> Torr.	0.0	0.0	0.0	0.0	0.7	.22
<i>Zizyphus garryi</i> Torr.	0.0	0.0	1.3	0.0	0.0	.45
<i>Quercus texana</i> Buckl.	0.0	0.0	0.0	5.2	0.0	3.15
<i>Quercus hypoleuca</i> Engelm.	0.0	0.0	0.0	1.3	0.0	.45
<i>Quercus durandii</i> Buckl.?	0.0	0.0	0.0	2.2	0.0	.75
<i>Quercus grisea</i> Lieb.?	0.0	0.0	34.2	43.4	83.2	50.69
<i>Forestiera parvifolia</i> (Gray) Small.	14.3	2.4	0.0	0.0	0.0	.37
<i>Forestiera pubescens</i> Nutt.	0.0	0.0	0.0	1.1	0.5	.24
<i>Forestiera neo-mexicana</i> Gray.	0.0	0.0	0.2	0.0	0.0	.07
<i>Prunus rivularis</i> Scheele.	0.0	0.0	0.2	0.0	0.0	.07
<i>Lycium berlandieri</i> Dunal	0.0	0.0	0.4	0.0	0.0	.15
<i>Rhus microphylla</i> Engelm.	0.0	0.0	1.1	0.0	0.0	.37
<i>Rhus trilobata</i> Nutt.	3.5	14.6	13.9	34.5	0.7	17.07
<i>Rhus leucantha</i> Jacq.	3.5	4.8	0.0	0.0	0.0	.22
<i>Ungnadia speciosa</i> Endl.	0.0	0.0	0.0	0.2	0.2	.15
<i>Clematis drummondii</i> Torr. & Gray	0.0	0.0	0.2	0.0	0.0	.07
<i>Fagara fruticosa</i> (Gray) Small.	7.1	0.0	0.0	0.0	0.7	.37
<i>Opuntia filipendula</i> Engelm.?	0.0	7.3	3.0	0.0	0.7	1.42
<i>Opuntia engelmanni</i> Salm	0.0	0.0	0.2	0.0	0.0	.07
<i>Opuntia leptocaulis</i> DC.	0.0	0.0	0.4	0.0	0.0	.15
<i>Opuntia davisii</i> Engelm.	0.0	2.4	0.2	0.0	0.0	.15
<i>Berberis trifoliata</i> Moric.	3.5	7.2	0.7	0.4	0.2	.75
<i>Cephalanthus occidentalis</i> L.	3.5	0.0	0.0	0.0	0.0	.07
<i>Baccharis salicina</i> Torr. & Gray.	0.0	2.4	0.0	0.0	0.0	.07
<i>Cercis occidentalis</i> Torr.	7.1	2.4	0.0	0.0	0.0	.22
<i>Lonicera albiflora</i> Torr. & Gray.	0.0	2.4	0.2	0.0	0.0	.15
<i>Ulmus americana</i> L.	10.7	0.0	0.0	0.0	0.0	.22
<i>Salix nigra</i> Marsh.	0.0	0.0	0.0	0.0	0.0	.00
<i>Coccolus carolinus</i> DC.	7.1	0.0	0.0	0.0	0.0	.15
<i>Amorpha fruticosa</i> L.	3.5	0.0	0.0	0.0	0.0	.07
<i>Artemisia filifolia</i> Torr.	0.0	7.3	0.0	0.0	0.0	.22

The vegetation of the floodplains along watercourses (fig. 2) is more mesophytic and shows a striking dissimilarity to the surrounding uplands both by having a much thicker stand of woody plants, and in having several species of woody plants not found in the more xerophytic regions.

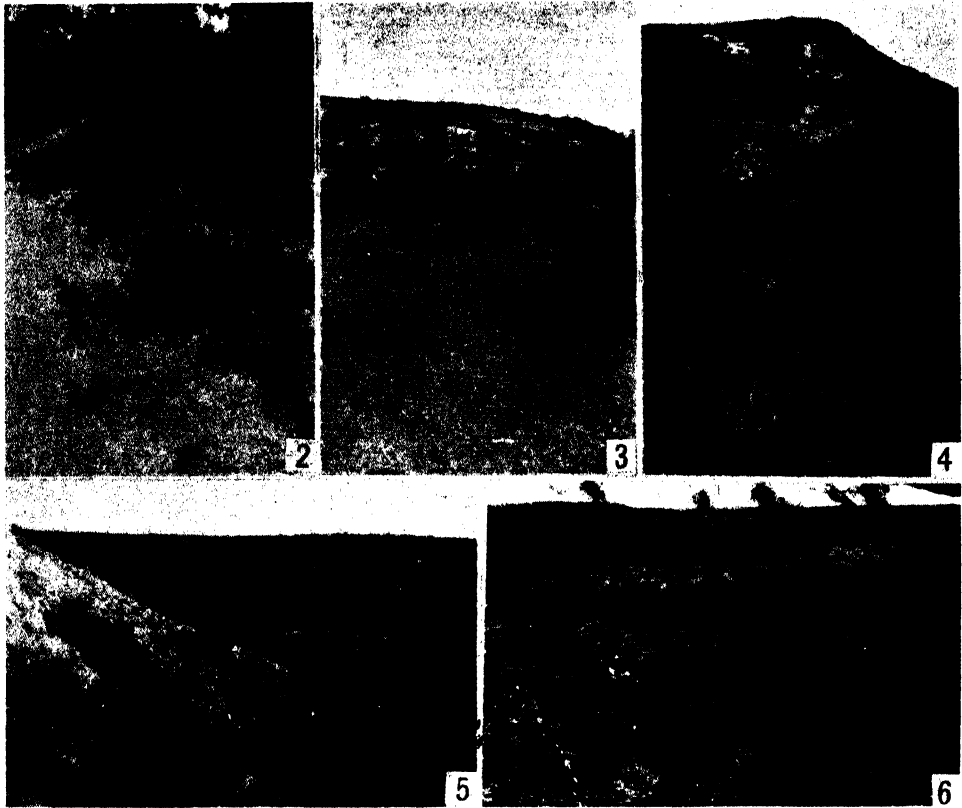


FIG. 2. View of the more mesophytic vegetation of the arroyo where the third and fourth counts were made; the shrub in the foreground is *Cephalanthus*.

FIG. 3. The low desert plains and the north side of the plateau which is covered with "shinnery" oak.

FIG. 4. The west exposure of the plateau along the route of the second count.

FIG. 5. The face of the plateau looking towards the southwest. The "shinnery" is abundant on the low plain and *Quercus texana* is seen in the background at the base of the plateau.

FIG. 6. The west side of the plateau showing the zonation at its base.

The author is indebted to Dr. G. J. Goodman and Mr. David Foster of the Department of Botany of the University of Oklahoma, Norman, Oklahoma, for their assistance in the field, and to Dr. J. M. Greenman and Miss Nell Horner, of the Missouri Botanical Garden, St. Louis, Missouri, for their assistance during the identification of the specimens which are deposited in the Herbarium of the Missouri Botanical Garden.

FRED A. BARKLEY

UNIVERSITY OF OKLAHOMA
AND

WASHINGTON UNIVERSITY, ST. LOUIS, MISSOURI

AN INQUILINE GAMMARID ON THE SEA-URCHIN *Lytechinus*

During some investigations of the locomotor activities of the common Bermudian sea-urchin *Lytechinus variegatus atlanticus* (A. Ag.) I noticed occasional, small, whitish bodies among the spines of the aboral region of this animal. They resembled most strikingly fragments of calcareous faeces which were often discharged by the sea-urchin. They differed from these, however, in that they adhered regularly to the outer portions of the spines and could not be dislodged from this location even by a jet of water strong enough to wash away other accumulated detritus. When one of these bodies was caught in a pipette and examined under a good hand-lens it was seen at once that what appeared to the unaided eye as a fragment of waste material was in reality a small amphipod that had adopted this rather unusual habitat. A systematic search was then made for these minute creatures with the result that from sixty sea-urchins twelve crustaceans were obtained. They were found almost invariably adhering to the more distal parts of the sea-urchin's spines and when an attempt was made to suck them off with a pipette they held to the spines with great pertinacity and often shifted their positions in such a way as to avoid being caught by the current of water.

The specimens collected by me were preserved in alcohol and on my return from Bermuda to the United States they were sent for determination to Mr. C. R. Shoemaker of the United States National Museum. Mr. Shoemaker kindly informed me that the species was *Amphilocus neapolitanus*, a form described in 1893 by Della Valle from a single specimen collected among the algal growths on the reef of the Posilipo off Naples. This species has since been taken in a number of other localities and is recorded by Chevreux and Fage (1925) as from the French coast both on the Atlantic and the Mediterranean sides, the North Sea, Great Britain, Tunis, Algiers, Canaries, coast of the Sahara, and Australia. Della Valle, at the same time that he described *A. neapolitanus*, also described another species from Naples, *A. brunneus*. The distribution of this species, according to Chevreux and Fage (1925, p. 115), is the French coast and the Mediterranean much as in the former species, and two distant points Lake Chilka (Bay of Bengal) and Bermuda. The latter locality was established by Kunkel who in 1910 described the amphipods of Bermuda. In this report (1910, p. 12) Kunkel states that several specimens of *A. brunneus* were taken at the Flatts Village, Bermuda, in sand from low water to two fathoms and that others were collected in Castle Harbor on dead coral. Mr. Shoemaker informs me that *A. brunneus* is now considered a synonym of *A. neapolitanus*; hence my own record is in reality a confirmation of Kunkel's. The exact location from which my material came was the Ferry Reach, a body of water bordering on West St. Georges and directly connected with Castle Harbor.

In all the references that I have been able to consult *A. neapolitanus* (as well as *A. brunneus*) is described as a free-living form associated with marine algae, dead coral, or sand. None of the various authors who have written on this species makes any reference to it as an inquiline, and no one remarks on its association with sea-urchins. Of the material that came to my hands all specimens were taken from *Lytechinus*. As already remarked it was with extreme difficulty that these gammarids were dislodged from the spines of the sea-urchin. After they had been sucked off in a pipette they would immediately swim back to the *Lytechinus* if they were liberated in its vicinity. This occurred again and again in an aquarium the floor of which was covered with coral sand onto which they might easily have settled. It was remarkable to see how directly they swam toward the sea-urchin if liberated within about five centimeters or less of it. If they were freed at a somewhat greater distance, they commonly swam about in a somewhat aimless way but if, in the course of this swimming, they came again near a sea-urchin, they were very sure to take a direct and final course toward it. In all these observations it seemed clear that *Amphilocus* made every effort to reach the sea-urchin. Having attained its goal the gammarid seized upon a spine near the distal end and

remained perched there well beyond the reach of the pedicellariae. The persistence with which *Amphilocus* sought out *Lytechinus* and the vigorous and active opposition that it showed to removal from this sea-urchin have led me to conclude that the gammarid is an inquiline species sessile on *Lytechinus*. It is remarkable that no other investigators have noted these peculiarities. They were so striking that I have been tempted to suspect that possibly there may be different races of this gammarid some of which are strictly free-living while others are inquiline, but on this point I have no particular evidence.

These observations were made at the Bermuda Biological Station for Research during February, 1935. I am under great obligations to the Director of this station, Dr. J. F. G. Wheeler, and his staff for the opportunities offered me to carry out my studies on *Amphilocus*. These were made while I was pursuing other investigations on the color changes of fishes under a grant from the Milton Fund of Harvard University.

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G. H. PARKER

BIOLOGICAL LABORATORIES,
 HARVARD UNIVERSITY

THE INTERNATIONAL OFFICE FOR THE PROTECTION OF NATURE

The Dutch and French Governments have now officially recognized the International Office for the Protection of Nature and have appointed the following delegates to be their representatives to the General Council of the Office:

Delegates for Netherlands and Dutch East Indies: *Dr. P. G. van Tienhoven*, President of the Society for Nature Protection in Netherlands; *Dr. W. A. J. M. van Waterschoot van der Gracht*, Chief Engineer of Mines; *Prof. Dr. L. Ph. le Cosquino de Bussy*, Director of the Colonial Institute, Amsterdam; *Dr. J. C. Koningsberger*, former Minister of Colonies.

Delegates for France and Colonies: *Mr. M. Bolle*, Conservator of Forests, Ministry of Agriculture, Paris; *Prof. Dr. A. Gruvel*, General Secretary of the National Committee for the Preservation of Fauna and Flora in the Colonies; *Mr. Raoul de Clermont*, President of the Section for Nature Protection of the Société Nationale d'Acclimatation de France.

Note.—Further information regarding this important movement may be found in the October, 1935 issue of this journal.¹ The International Office is at Brussels and the American Committee for International Wild Life Protection, Cambridge, Massachusetts, will receive contributions which are needed for the support of the various activities of the Office.

THE EDITORS

¹ **Shelford, V. E.** 1935. International preservation of nature. *Ecology* 16: 662-663.

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INDIGENE VERSUS ALIEN IN THE NEW ZEALAND PLANT WORLD

H. H. ALLAN

Plant Research Station, Palmerston North, New Zealand

Magna est veritas et praevalebit, but the struggle is often prolonged, and when at long last the campaign seems over, the enemy may return to the charge. Perhaps Pilate was not jesting when he would not stay for an answer to that difficult question, "What is truth?" It was natural for Hooker (1867) to be so impressed by the apparently steady advance of alien plants into New Zealand in ever increasing hordes as to think that "many plants, which, though unknown in the islands a quarter of a century ago, are already actually driving the native plants out of the country." It is not surprising that Darwin (1872) and Wallace (1880) should seize on this supposed all-conquering progress of "European productions" as an extremely important phytogeographical fact with evolutionary significance. Darwin, who certainly always includes animals in his argument, makes a surmise, calls it a result, and the fact of the superiority of the aliens is taken as established. Wallace (1905), with less than his usual acumen, swallows several tall stories and the argument is considered clinched. It is understandable that Travers (1870) and even Kirk (1896) could not altogether free themselves from the weight of these authoritative names, but one had expected that the accumulated observations of later years, especially the careful examination of Thomson ('22) and the vigorous exposition of Cockayne ('28), could have enabled overseas as well as local botanists to get matters into proper perspective. It was with a shock of surprise, therefore, that one found in a valuable paper by Rübel ('35) New Zealand advanced in support of the following argument: "A species or an association may be adapted to a climate and may thrive in a soil when not limited in space, but it may lack strength to compete with new invaders. To be successful it must not only possess ability to thrive but also in addition the power to combat competitors. Only if the environment is sufficiently favourable to give strength enough to enable the plant to resist competition is the minimum necessary for success attained. *For instance,*

in New Zealand the old established vegetation has been expelled by invaders that have come in with the white man. These invaders have increased by their competition the necessary minimum above the favourable environment formerly present. This has caused a change, a dispossession." (Italics mine.)

Whatever the strength of Rübel's thesis, the instance given is an unfortunate one, if as seems intended this dispossession is to be understood as the result of competition between alien and indigenous plants on fairly level terms. On the other hand it is perfectly true that the changes in the New Zealand vegetation afford an important field for that study of which Tansley ('35) has remarked: "Regarded as an exceptionally powerful biotic factor which increasingly upsets the equilibrium of preexisting ecosystems and eventually destroys them, at the same time forming new ones of very different nature, human activity finds its proper place in ecology."

It is not possible to state precisely how many species of plants are actually naturalized in New Zealand; much depends upon the view taken as to what constitutes naturalization, and for a number of species definite information is lacking. Hooker (1855) listed 61 species, and later (1867) 170. Kirk (1870) recorded 292. Cheeseman ('06) gave 528, and later ('25) 576, but a number of the species in his lists do not conform to his statement that they "appear to be thoroughly well established." Thomson ('22) considered that "over *six hundred species* have become more or less truly wild, *i.e.*, they reproduce themselves by seed, and appear at the present time more or less denizens of the country." But many of these are decidedly in the "less" class, and Cockayne ('28) accepts 514 as "more or less firmly established," but considers that his estimate "might be somewhat reduced with advantage." My own estimate of thoroughly naturalized species is 413, based on the evidence that they (1) occupy significant extents of territory, so that they are not liable to extinction by a small local catastrophe, (2) reproduce themselves, whether by seed or vegetatively, (3) are not decreasing in area occupied.

But for the purposes of this paper it matters little which estimate be adopted, and I have accepted 603 species. Now, in regard to competition with indigenes, 324 may be at once be put aside. They are either rare or so local and limited in extent as not to play any significant part in the struggle. Of the remainder no fewer than 231 (including 165 annuals or biennials) occur mainly in waste places about settled areas, cultivated lands and man-made pastures, and only 93 of them extend into very much modified indigenous communities (especially low tussock-grassland and coastal sands). None of them sets up any serious competition with the indigenes. There remain to consider 48 species only. Of these 28 are of Old World origin, 9 are from the Americas, 7 from Australia, and 4 from South Africa. The life-forms are: 1 parasitic plant, 4 water plants, 22 shrubs and trees, 4 grasses, and 17 perennial herbs or half-shrubs.

Cuscuta epithymum has established itself on a number of indigenous

species, especially on certain salt-meadows and river-terraces, but has not ousted any indigene nor been a serious detriment to any of its hosts. Of the water plants *Anacharis canadensis*, *Nasturtium officinale* and *Ranunculus fluitans* are widespread in lowland waters the vegetation of which was for the most part already much altered by man and his stock before their advent. *Aponogeton distachyus* has recently spread rather widely, aided to some extent by planting, in small streams and ponds in North Island. It is probable that *N. officinale* has locally suppressed indigenes on stream-margins. None of these water plants is of any special moment in montane areas, and no indigene is in the slightest danger of extinction by them. While numerous grasses have established themselves in lowland tussock-grassland subject to the influences of stock and fire, and while many have secured a place in such open communities as coastal sands, burnt-over heath and river-beds, only 4 have any claims as suppressors of indigenes—*Agrostis tenuis*, *Ammophila arenaria*, *Eragrostis brownii*, and *Sporobolus capensis*. In certain low tussock-grasslands that have long carried stock and long been subjected to fire *A. tenuis* forms areas of dense turf suppressing smaller species. But in tussock-grassland that has been little disturbed it is of only occasional occurrence. In spite of the 90 odd invaders even greatly modified grassland still bears the majority of its indigenes. *A. arenaria* has been extensively planted in sand-dune country and has spread naturally in many places, but has not succeeded in endangering the hold of any indigene except where planted in its thousands. *E. brownii* and *S. capensis* have shown themselves well suited to become important members of induced grassland on heath country, and to a lesser extent in low tussock-grassland, but neither has successfully invaded undisturbed indigenous communities.

It is among the shrubs that are to be found the most imposing invaders. To see whole hillsides, as in the neighbourhood of Wellington, ablaze with the gorse, *Ulex europaeus*, certainly gives one the impression of a highly successful alien. But consider the process of events. The hills wore a primeval covering of dense coastal forest. The forest was felled, the lumber burnt, and the area sown with "European" grasses. The pasture resulting, with its weeds, was invaded not by further aliens in the first place but by indigenes of the genus *Danthonia*. The *Danthonia* grassland has been burnt over and in turn, in places, invaded by the gorse. Here, truly, large areas of an indigenous-induced association have been conquered by an alien. But enclose a piece of gorse thicket, keep fire and stock away, and the gorse begins to weaken, allows the entry of indigenes, and a distinct tendency is seen towards the establishment of forest. Locally also (Allan, '26) *U. europaeus* may dominate modified tussock-grassland and suppress the indigenes. Open stony river-beds have in places become dominated by *Cytisus scoparius*, *U. europaeus* or *Lupinus arboreus*, and the latter occupies much ground in coastal sandy country, where it has been extensively sown. But the total area occupied by these species is comparatively small. *Hakea acicularis* and *Erica*

arborea have spread remarkably in burnt over heath country in North Island, and have become important members of the communities, often sharing dominance with the indigenes. In many parts, especially of South Island, areas that once carried forest, have on attempts at pasture formation, become dominated by *Rubus fruticosus* (in a wide sense), but, again, no unmodified community has been seriously affected by these species. On modified heath, bush-burn pastures, and in various induced communities other shrubs have locally produced thickets or have become important members of the new vegetation, without making any significant impression on unmodified vegetation. These are: *Acacia armata*, *A. decurrens*, *Albizzia lophantha*, *Cytisus candicans*, *Hakea saligna*, *H. suaveolens*, *Hypericum androsaemum*, *Lantana camara*, *Leycesteria formosa*, *Lycium horridum*, *Pinus radiata*, *Psoralea pinnata*, *Ribes grossularia*, *Rosa eglanteria*, and *Sambucus nigra*. But of all this list it has to be said that they have only secured their stands in areas where man has greatly assisted in the fight, wittingly or unwittingly. Several, indeed, have only established themselves effectively in man-made communities.

Of the 17 herbs none have proved to seriously endanger the existence of any indigenous species let alone community. *Eschscholzia californica* has spread widely on open stony riverbeds in many places in South Island, where under primitive conditions the vegetation was sparse and subject to wiping out by floods. But even where the *Eschscholzia* has become dominant the indigenes still retain their places. *Cirsium arvense* has become a striking feature of parts of Central Otago, where man's activities have resulted in a more or less desert formation, and is accompanied by many other weed aliens. But even here the indigenes are reasserting themselves, while over a considerable part of this induced "steppe" area the indigenes have taken the premier part in the successions now taking place. *C. arvense* is also locally abundant in certain bush-burn pastures, where also *Digitalis purpurea* may be prominent for a time, while *Eupatorium glandulosum* is at present a great nuisance in similar country in North Auckland, as is *Senecio jacobaea*. But their aggressiveness has not been at the expense of indigenes but of other aliens. *Plantago coronopus* often occurs in dense masses in coastal salt-meadow, and locally may have possibly suppressed indigenes, as may *Trifolium repens* in lowland tussock-grassland. *Verbascum thapsus* occurs freely in open stony places, but has neither suppressed any indigene nor taken any real place in closed communities. *Aster subulatus* (salt-meadow), *Galega officinalis* (riverside pasture and riverbed), *Hypericum perforatum* (bush-burn and other grassland), *Oenothera odorata* (pasture on sandy areas), and a few other aliens are locally very prominent, but, once again, only where man's influence has been considerable. In very much damaged lowland forest, *Tradescantia fluminensis* in certain localities forms a dense cover, suppressing the floor-vegetation. Thus, for none of the herbs can a really good case be made out for their aggressiveness as against indigenes, without the help of man and his animals.

Communities above the forest-line, even where long subjected to burning, remain remarkably free from aliens, though these may be noted along tracks and by camping places (whether of man or of animals). *Rumex acetosella* is able to find a place in a surprising number of disturbed communities and to reach a considerable altitude, as does *Hypochaeris radicata*, but never to the menace of an indigene. The outstanding result is not at all the aggressiveness of aliens, but the power of indigenous communities to resist their entry. Thomson ('22) quite truly remarks: "No instance can be recorded of any species of native plant which has been exterminated owing to this (action of animals) or any other cause dependent on European occupation of the islands." Cockayne ('28) is equally justified in his statement: "wherever any part of New Zealand is in its primitive condition and uninterfered with by man or the animals he has introduced, none of the exotics have gained a foothold, their great powers of dissemination notwithstanding, although the virgin area may be pierced in all directions by ground occupied by man where there are introduced species in plenty." Local extermination of vegetation has of course taken place, but not through the action of alien plant upon indigene pure and simple but by man armed with axe and firestick, plough and drill and seed-bag, assisted by his horses, cattle, sheep and goats, abetted by rabbits, deer and what not. We are left with the result that only some half dozen aliens can truly be said to have suppressed any indigene—and that very locally.

So much for the obverse of the medal; what of the reverse? So far from the indigenes being unable to halt the aliens we find, under the very conditions that man has imposed and greatly to his distaste, a most remarkable increase of a number of indigenes and the establishment of a set of new communities, some of very wide extent, dominated by them. Outstanding among these are the great grassland areas now dominated by species of *Danthonia*, the very extensive heaths of *Pteridium esculentum*, *Leptosperum scoparium* and species of *Cassinia*, where "European" grassland had been the aim of the pastoralist. Very noteworthy also are the areas that have been overrun by *Aristotelia serrata*, *Brachyglottis repanda*, species of *Coriaria*, *Fuchsia excorticata* and other forest species in pure or mixed stands. Of great aggressiveness also, among others, are species of *Acaena*, *Blechnum procerum*, species of *Cyathea* and *Dicksonia*, *Histiopteris incisa* and *Paesia scaberula*.

In tussock-grassland burning has resulted in a number of localities in a marked increase of species of *Celmisia*, especially *C. spectabilis*, and *Chrysobactron hookeri*. Partial draining of swamps has led to great fields of *Phormium tenax* and the increase of *Arundo conspicua*. In mountain areas we have the phenomenon of burnt forest being replaced by grassland, herb-field, fellfield or shrubland composed of indigenes. Details of this new vegetation are readily available in Cockayne ('28) and Cockayne, Simpson and Thomson ('32). Levy ('23) has given a good illustrated account of such changes in a particular area, while Moore and Cranwell ('34) have

described a very remarkable instance of *Microlaena avenacea* grassland taking the place of forest owing to the action of introduced animals in the absence of felling and burning. There is evidence on every hand to support Cockayne's conclusion: "In fact, it is hardly going too far to declare, that were such animals entirely removed from North Island, the whole of the present 'permanent pastures' would in one hundred years, or less, be well on the road once more towards dense rain-forest." The greatest enemies of the pastoralist in New Zealand are the indigenous not the alien weeds.

The term "induced" has been used in the sense of Cockayne: "made directly or indirectly by man's action." We find in the New Zealand of to-day three distinct classes of communities:

1. *The artificial-induced*—directly made by man after the destruction of the primitive vegetation, and occupying the greater part of the more closely-settled areas.

2. *The primitive* (in part modified to a greater or a lesser extent)—now mainly confined to the sparsely settled areas and the mountain regions.

3. *The induced* (partly *exotic*, but largely *indigenous-induced*)—occurring to a considerable extent, especially the indigenous, as an interrupted tension-belt between 1 and 2, against which the land-occupier has to wage incessant warfare.

If all the introduced fauna were removed the evidence strongly favours the view that the aliens would be conquered by the indigenes, surviving only in greatly reduced numbers and as very subordinate members of the resulting ecosystem. As the Maori made but little impress on the primitive vegetation and would revert to something like his ancestral habits, he might be allowed to remain to report progress!

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NOTES ON AN AMERICAN CAVE FLATWORM,
SPHALLOPLANA PERCAECA (PACKARD)

J. WILLIAM BUCHANAN

Northwestern University

INTRODUCTION

This is an account of certain observations I have been able to make on the behavior and on some of the physiological characteristics of the American cave flatworm, *Sphalloplana percaeca* (Packard). The conclusions are but tentative; many of the tests and experiments to which the animals were subjected are quite incomplete, for this interesting form is obtainable only in small numbers and with considerable difficulty. But within the limits imposed by the smallness of the number available and other difficulties that will become apparent farther on, the data appear to contribute to the knowledge of cavernicolous animals in general and to that of the paludicolous Turbellaria in particular.

This particular American cave triclad seems to have been first described from Mammoth Cave by Packard in 1879 and named *Dendrocoelum percaecum*; it is inadequately figured in the various editions of his textbook beginning with the 1880 edition (page 141). References to its anatomy and taxonomic position are to be found in Packard's papers ('79, '88), in Spandel ('26), Chappuis ('27), Hyman ('31), de Beauchamp (Bolivar et Jeannel, '31), Wolf ('34), and Castle and Hyman ('34). I find no reference to this form in von Graf's treatise in Bronn's *Klassen und Ordnungen des Tierreichs* ('12-'17).

In general, the classification of the triclad flatworms is in an unsatisfactory state, for so far no very accurate criteria have been established and the validity of the characteristics described as taxonomic bases by various authorities has not been universally accepted. Moreover, the position of this cave form in the tentative taxonomic groups is uncertain. The records of Packard (*loc. cit.*) placed it in the genus *Dendrocoelum*. But if the families of triclads are to be distinguished by the arrangement of the muscle fibres of the inner zone of the pharynx (Kenk, '30, p. 151), this triclad is properly placed in the family Planariidae, for the muscle fibres in the inner muscle zone of the pharynx are not intermingled as in the Dendrocoelidae, but form two distinct layers of longitudinal and circular elements (Hyman, '31). A serious objection to Kenk's classification of families based on this difference in muscle arrangement may be raised, namely, that an acceptance of these differences as distinguishing families must forever limit the number of pos-

sible families of triclads to two only. Pending further analysis of the group, Kenk's classification may be profitably adopted and the cave form regarded as in the family Planariidae. Hyman (*loc. cit.*) regards the animal as properly belonging in the genus *Fondicola* because of its head shape and the nature of the entrance of the common oviduct into the atrium. More recently de Beauchamp has established a new genus, *Sphalloplana*, to provide for this unusual form (Bolivar et Jeannel, '31). Wolf ('34) in his comprehensive *Animalium Cavernarum Catalogus* accepts de Beauchamp's classification (p. 21) and makes no reference to the work of Hyman.

It is not proposed here to re-describe the anatomy of *Sphalloplana percaeca*, nor to question the morphological basis of its present taxonomic position. It seems of some value to determine which epigeic triclad it most closely resembles in behavior and in physiological characteristics, for quite obviously its nearest relative are unknown. They may be found either among the Planariidae, particularly within the genus *Fondicola* (Hyman, '31) or, according to the older classification of Packard ('79), among certain genera of the family Dendrocoelidae. I had available for comparisons *Fondicola* (*Phagocata*) *gracilis*, and *Procotyla fluviatilis* (formerly known as *Dendrocoelum graffi*) and made certain incidental observations on the behavior of two species of *Euplanaria*, *E. dorotocephala* and *E. maculata*. Unfortunately *F. velata* and *F. truncata*, both occurring in the geographical area which includes the Kentucky caves, were not available.

PROBLEMS

Figures 1, 2, and 3 enable one to appreciate the resemblances and differences between these three forms in their natural and living state as seen under low magnification. It will be seen that *S. percaeca* (fig. 1) rather closely resembles the white epigeic *P. fluviatilis* (fig. 2); the resemblance is especially close if *S. percaeca* is compared with a partially starved *P. fluviatilis*, in which the digestive tract is free from pigmented contents and the margins of the animal no longer crenulated. The location and character of the cotyledons are much the same, the shapes of the heads and bodies quite similar, and there is some resemblance in the arrangement of the digestive systems as seen through the body wall. Of course the eyes, quite conspicuous in *P. fluviatilis*, are totally lacking in *S. percaeca*. The digestive system of *S. percaeca* does not extend quite as far anteriorly as that of *P. fluviatilis*, and in the former, under suitable lighting, the nerve tracts and cephalic ganglia are discernible through the body wall of the head. When *S. percaeca* and *F. gracilis* (fig. 3) are compared in the living state (de Beauchamp's figure was drawn from preserved material) the resemblances are only of the most general character. Quite clearly the head of *S. percaeca* is not that of a *Fondicola*, an anterior sucker is absent in *F. gracilis*, and the general body shapes and arrangement of the digestive systems are distinctly different. The fact

that this particular species of the genus *Fondicola* has the unusual feature of multiple pharynges renders comparison of their digestive systems of little worth; but it will be agreed that from their externally observable characters the two forms do not appear to be as closely related as do *S. percaeca* and *P. fluviatilis*.

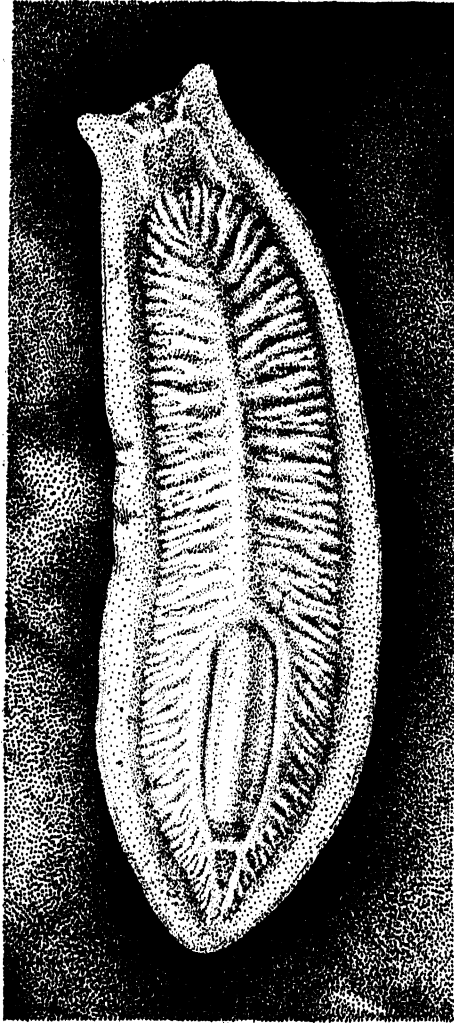


FIG. 1. *Sphalloplana percaeca* (Packard). Drawn from a living specimen ten days after collection. Length, 12 mm.

General similarities and dissimilarities of this sort are commonly regarded as of little value in determining taxonomic relationships. The question of the possible remote derivation at least, if not relationship, of the cave form may be approached from the study of its reactions. The assumption may be made that the ancestors of the cave flatworms entered the cave¹ at some time

¹ The animals of Mammoth Cave are said to be post-glacial inhabitants. See Eigenmann, '08.

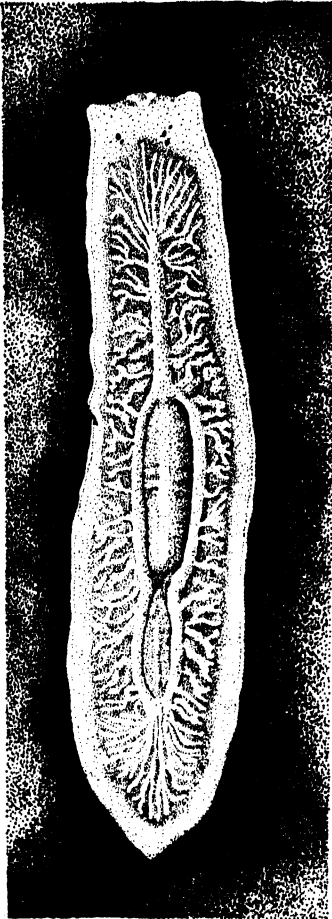


FIG. 2.

FIG. 2. *Procotyla fluviatilis* Leidy. Drawn from a living specimen after two months starvation. Length, 12 mm.



FIG. 3.

FIG. 3. *Fondicola gracilis* Leidy. Drawn from a living specimen after two weeks starvation. Length, 12 mm.

or another equipped with reaction systems not greatly different from those of present day epigeic forms. That the milieu influences materially the feeding habits, reaction to light, to temperature, and other activities of many animals is generally agreed. The question of the effect of possibly a million years of cave conditions upon these responses in a simple aquatic form immediately suggests itself. Specifically, which epigeic group does the cave animal most closely resemble with respect to its reaction to light, to water temperature and pressure, to acidity, to reduced oxygen supply, in regenerative capacity, in feeding habits, and in righting and orienting reactions? Does the cave form exhibit responses that are different in character from those of the surface living animals? Unquestionably both physiological and morphological char-

acters are to some extent at least determined by the habitat of the animal. Does the cave flatworm differ only morphologically from the epigeal forms? It is here that we encounter the debated question as to whether morphological characters alone furnish the basis of classification. But a study of the physiological characteristics of *S. percaeca* may furnish facts that will be contributory at least to the establishment of its true taxonomic position.

The high powers of regeneration of many American members of the family Planariidae are well known. The *Euplanaria* are commonly employed in student laboratories to demonstrate reconstitution, and recently the capacity for regeneration of two members of the genus *Fondicola* has been described with some completeness (Castle, '28; Buchanan, '33). On the other hand, members of the Dendrocoelidae have limited capacity for reconstitution (Lillie, '01; Sivickis, '31). It is contributory to the general problem to know which of these two groups *S. percaeca* more closely resembles in this respect. Regenerative capacity in triclads has been referred to the presence of certain specific cells by Curtis and his co-workers (Curtis and Schulze, '24) and to the ability of the tissues or certain of them to respond to the stimulus of injury by setting up a differential in physiological state that results in re-establishment of the individual by de-differentiation and development (Child, '21). With the extremely limited number of animals available, my observations on regeneration in *S. percaeca* throw no light on this problem. But they do answer the question as to whether or not the highly special cave environment has operated to alter materially the regenerative capacity of the animal, or at least the question as to whether or not the cave animal differs markedly in this regard from forms that have not been subjected to age-long cave conditions. Cave flatworms are isolated entirely from light changes, are subjected to only minor temperature changes, are withdrawn completely from dangers due to the feeding habits of aquatic birds. They may furnish some of the food supply of small fish, amphibia, and crustaceae and are no doubt endangered by rolling rocks and rapid currents, but in general they are not subjected to the variety of hazards the epigeal flatworms encounter.

Paludicolous flatworms are in nature constantly in danger of being swept to greater depths, particularly under waterfalls and in rapid currents. Some of the epigeal forms orient and return to normal habitats because of their negative reaction to gravity in water with deficient oxygen supply, in foul water, and under abnormally high hydrostatic pressure. My supply of *S. percaeca* was obtained from rocks in a small stream fed by a thirty foot waterfall; consequently I was interested in their orientations with respect to these possible conditions in their environment. Moreover, it was of further interest to determine their orientations to acid and alkali, to water current, to possible foods, and to light and temperature.

In epigeal *Euplanaria* and *Fondicola* a physiological polarity is expressed by antero-posterior differences in permeability of the integument, in susceptibility to toxic agents, in capacity and rate of regeneration, and other criteria

of physiological condition. It is of value to extend these studies to the cave form, first to add to knowledge concerning the form itself, and secondly, to determine whether these aspects of the organism are materially different in an animal with prolonged existence in a selected habitat of this character, that is to say, a habitat devoid of light and with only minor temperature changes.

The study of these and other related questions in this unusual animal has been at least fascinating and has yielded some clear answers even though the number of animals has not made it possible to make exhaustive tests. But little aid is given in answering the questions raised by Dudich (in the *Einleitung, Animalium Cavernarum Catalogus*, Wolf, '34) as to the age of the cave animals, the stems from which they originated, how they arrived at the cave habitat, and whether their differences from epigean forms are due to gene changes or adaptation. Similar questions have brought forth partial or speculative answers from most investigators who have interested themselves in cave forms, *c. g.*, Spencer, Lankester, Eigenmann, and still earlier, Tellkamp in 1845 (see Eigenmann, '08).

MATERIALS

Forty living specimens of *Sphalloplana percaeca* taken at different times from under rocks under and near a waterfall of approximately thirty feet in Annette's Dome at the two hundred foot level in Mammoth Cave, Kentucky, have come to my laboratory.² I have been able to make observations on the animals in cave water kept at approximately the cave temperature within forty-eight hours after their capture. It was soon found that tap water served just as well; some starving animals have been kept for about two months in cool tap water without any evidence that their behavior or physiological condition was adversely affected by the water. As a result of certain observations on the effect of light it was deemed advisable to keep the animals in darkness or in weak diffused light. For purposes of comparison, cultures of the following were secured and kept under the same conditions: *Euplanaria dorotocephala*, *Euplanaria maculata*, *Fondicola gracilis*, and *Procotyla fluviatilis*. Except for incidental observations, attention was focused on comparisons in behavior between *S. percaeca* and *P. fluviatilis* and *F. gracilis*, with particular reference to that of *S. percaeca*. I propose to give my observations here in the form of a running account taken and re-arranged from my notes set down at the time of each examination.

² Professors C. L. Turner and Orlando Park, of this department, collected and sent me the first lot of cave flatworms. I am further indebted to Professor Park for the identification of some of the cave animals and other assistance. Cheerful acknowledgment is made of the intelligent help of Mr. Schuyler Hunt, a guide in Mammoth Cave for the past forty years. His cooperation has been made possible the assembling of a very complete collection of the fauna of Mammoth Cave by this laboratory.

GENERAL OBSERVATIONS ON *Sphalloplana percaeca*

Of the forty specimens handled, only one measured as much as sixteen millimeters in the living condition; the usual size was approximately ten millimeters. This seems to be the size of animals from this particular collecting ground; seasonal differences are not apparent for one lot was received in early April, one in late June, and one was collected by myself in November. The water temperature in Annette's Dome was, in April, 14° C. and in November 12° C. Reliable information is that the temperature of the water does not change beyond these two readings. The hydrogen ion concentration as determined by colorimetric methods was pH 7.6. The animals were found clinging to the under side of rocks submerged in water and were somewhat difficult to obtain, for their collection was made possible only by the fact that running subterranean waters occasionally cross accessible paths. None were found in still waters nor in sandy places. No doubt they are widely distributed in underground streams but this statement must continue to lack confirmation. I am quite unable to confirm the statement of Giovannoli ('33) that this form is abundant in the waters of Mammoth Cave, particularly in Richardson's Spring. A careful search of this spring and the waters thereabout failed to discover any *S. percaeca*. It is, of course, easily possible that the animals are less numerous than formerly, although probably never common. Packard evidently did not find it on his first trip to Mammoth Cave ('71) but in a later paper ('88) mentions its presence in Richardson's Spring and in Gothic Avenue. Banta ('07) mentions finding *S. percaeca* in Mammoth and a nearby cave.

Banta's remark ('05) that the habit of hiding under loose stones and other debris persists in many cave forms where the habit is useless, does not apply to *S. percaeca*. It seems much more probable that the flatworms are located on the nether side of rocks because they are deposited there by water currents and because the same currents deposit under the rocks the materials which furnish their subsistence.

LOCOMOTION

Ciliary creeping is comparatively rapid; the animals are more active than either of the two types of *Euplanaria* with which they were compared and much more active than *P. fluviatilis*. *F. gracilis* of comparable size are quite as active as the cave animals. *S. percaeca*, while in motion, performs the undulating movements of the body margins that characterize locomotion in *P. fluviatilis*. While the animal is in motion the auricles are quite distinct and pointed, a feature that closely resembles *P. fluviatilis*. The auricles are almost completely lacking in *F. gracilis*, as an examination of figure 3 will show.

RIGHTING REACTION

When *S. percaeca* are inverted in a dish of water one centimeter deep a relatively long time is required for righting. In successive trials with three different animals about seven millimeters long the times from inversion to complete righting were, in seconds: 60, 40, 60, 40, 40, 35, 22, 20, 50. Similar trials with *P. fluviatilis* yielded the following times: 40, 20, 10, 10, 15. *F. gracilis* rights itself with great promptness; successive trials with small animals were all completed within ten seconds. The data distinctly show that the time required for the coördinated effort of righting in response to the inverted position differs between different species under the same experimental conditions and that the cave animal is slower in this response than are the epigean forms. May this difference be attributed to their age-long existence in an environment in which they infrequently experience accident or displacement?

REACTION TO GRAVITY

Observed in air-saturated clean water in Erlenmeyer flasks, *S. percaeca* appeared indifferent to gravity and located without apparent choice on the bottom and wall of the flask. When agitated the animals showed a tendency to leave the water and creep about above the water level. This tendency seemed more marked than in epigean forms and suggests an association with the fact that the air of the cave habitat registers 95 per cent relative humidity.

Reaction to Gravity in Low Oxygen Tension

A glass Y tube was constructed with arms about fourteen inches long and three-fourths of an inch in diameter. The base of the Y was closed by a short length of rubber tube and a pinch cock. The tube was then filled with boiling tap water and the arms of the Y sealed with rubber tubing and rubber bulbs filled with boiling water to allow for contraction during cooling. The assembly was then placed in the cold tank and cooled to the temperature of the flasks containing the *S. percaeca* stock. Four *S. percaeca* were then placed in a short test tube in cooled boiled water and the tube attached to the stem of the Y tube and the pinch cock removed. One arm of the Y was left sealed and the other was opened to the air and the whole submerged to the level of the open arm in a cold bath in dim light. Care was exercised to avoid agitation of the boiled water and exposure to air during the setting up of the apparatus. After twelve hours the animals had left the floor of the test tube and were in the stem of the Y. After twenty-four hours one animal was eight inches up in the closed arm of the Y tube; the others were still in the stem or had returned to the side wall of the test tube at the base. The experiment was repeated using a fermentation tube filled with cooled boiled water instead of the Y tube. By means of a needle the animals were placed at the lowest level of the tube. After twenty-four hours one animal had mounted three inches in the closed arm of the tube; the others remained quiet

near the point they had been inserted. The observations indicate that *S. percaeca* does not react to gravity when the oxygen concentration of the water is low.

The experiments were repeated with *P. fluviatilis*. After five hours, three of the four animals had mounted to the extreme upper end of the closed arm of the tube; the other one remained near its original location at the bottom. Eighteen hours later, however, all four animals were located near the surface of the open arm at points near the entering oxygen supply. Repetitions of this experiment gave results of the same character. The facts suggest that the first response of *P. fluviatilis* to low oxygen concentration is in the nature of a negative to gravity response.

Repetition of these experiments with *E. dorocephala* and *F. gracilis* were not decisive. Both of these forms move about restlessly when disturbed and tend to move upward in any container regardless of the oxygen tension of the water. The narrow limits of the tube diameter apparently directs their path so that they appear to react more markedly than is actually the case.

Reaction to Gravity in Oxygen-Saturated Water

Seven *S. percaeca* were placed in a one liter Erlenmeyer flask half filled with cold tap water, air-saturated. The flask was then stoppered and laid on its side in the cold water bath. After the animals had come to rest the flask was rotated very gently until the animals were disposed in an inverted position in the air. Random movements began within two minutes in four of the seven animals; the other three remained quiet for several minutes longer. It was observed that the movements were without orientation with respect to gravity, nor to the slope of the glass surface over which they were creeping. The course of any animal might be at one time up and at another time down, or again at right angles to the incline of the wall of the flask. Or an animal might creep up or down or across the flask bottom in its perpendicular position. The movements were persisted in by all the animals and within ten minutes all had entered the water. After repetitions I could only conclude from their behavior that the passing of the surface film over their dorsal surface, or their exposure to air, induces movements that appear to have no relation to gravity but which in this case eventually results in their return to water.

Reaction to Gravity in Foul Water

It has been the common observation in caring for laboratory stocks of *E. dorocephala* and of *F. gracilis* that when the water in the stock pans becomes stale or is fouled by decay of food, the animals seek the surface, evidencing a negative to gravity response that is unmistakable. The behavior of *S. percaeca* in the presence of foul water was tested by filling a flask with water drawn from a stock pan in which *E. dorocephala* had been kept and fed and had been allowed to become stale so that the *Euplanaria* showed an immediate

and rapid upward creeping reaction when placed in the flask. Several *S. percaeca* were inserted at the bottom of the flask but they were quite indifferent, remaining disposed about the floor while the *E. dorocephala* promptly mounted to the surface and remained there. In a similar test applied to *P. fluviatilis*, they, too, were indifferent at first but eventually crept to points near the surface.

Reaction to Water Pressure

On the assumption that *S. percaeca*, as well as the more familiar outside living flatworms are from time to time swept to deep water from which they return to normal habitat, and not being able to demonstrate a reaction to gravity in previous tests, the possibility came to mind that increased water pressure might elicit some sort of response. Accordingly, *S. percaeca* were subjected to some simple water pressure tests. A glass tube about three-quarters of an inch inside diameter and five feet long was fitted at one end with a short rubber tube connection and pinch cock. It was then filled with water and set erect in diffuse light. A test tube of corresponding bore was filled with water and in it were placed four *S. percaeca*. The test tube was then connected by means of the rubber tube with the bottom of the five foot water column and the pinch cock removed. The animals moved about in the test tube but did not mount higher. After an hour all were recovered in the test tube. The experiment was repeated with *F. gracilis*, *E. dorocephala*, *E. maculata* and *P. fluviatilis*. The observations were as follows:

F. gracilis: Seven out of ten animals mounted to within one foot of the top within an hour, but after twenty-four hours had redistributed themselves over the five foot range.

E. dorocephala: Out of ten animals all left the test tube within an hour and at the end of ten hours were all distributed in the upper half of the tube.

E. maculata: All of the animals left the test tube within an hour and distributed throughout the length of the column.

P. fluviatilis: All of the animals left the test tube and moved to the upper half of the column.

It may not be assumed that the upward creeping of these animals was a direct response to water pressure, but the results do show that *S. percaeca* is quite unresponsive to gravity under such pressure conditions and that the other forms react more or less actively to bring themselves nearer the surface. To test more thoroughly the possible effect of water pressure a thick walled test tube containing the animals was connected by means of pressure tubing to a faucet on a water line with a gauge reading of twenty pounds per square inch. The faucet was then turned on. In no case was there evidence of disturbance among the animals. In fact, the *S. percaeca* did not move during a half hour observation; the other forms moved about as under normal conditions.

From the observations in the several tests of the reaction of *S. percaeca*

to gravity it was necessary to conclude that gravity evokes no appreciable response, neither under normal conditions of water content nor under conditions of abnormal water and water pressure. In this respect it differs markedly from *Euplanaria* and *Fondicola* and less so from *P. fluviatilis*.

From these imperfect observations I am unable to come to any conclusions as to whether the cave animal will return to its normal position in the cave streams if swept to deeper water.

REACTION TO WATER CURRENTS

Four animals were placed in a trough with a water film flowing at approximately one foot per second. The movements of the animals appeared to have no relation to the direction of water flow. The observation was repeated at least five times. Observations were also made on single individuals in shallow dishes by passing a current from a pipette over the animal. Without doubt the animals are stimulated by the current but the direction of their movements is without orientation.

REACTION TO ACID AND ALKALI

A trough twenty inches long and eight inches wide with a glass bottom was placed over white paper. The trough was then filled with tap water colored with phenol red and the indicator adjusted to pH 7.6, which is the H ion concentration of the cave water from which the animals had been collected. I then placed four animals in the center of the trough and at one end dropped in several drops of N/20 NaOH. At the other end several drops of N/20 HCl were added. Gentle stirring soon established a color gradient against the white background. The animals wandered at random about the trough, appearing to be indifferent to the changes in H ion concentration as they approached the ends of the container. They finally came to rest in widely separated positions without any reference to the H ion concentration of their location.

In another experiment using the colored water in the trough as above, individuals were surrounded with an acid ring, observable by reason of the color differences. The animals crept directly out through the acid border without giving any indication of response as they encountered the acidity change. It seemed clear that within the pH range of the phenol red indicator *S. percaeca* is indifferent to H ion concentration.

In another experiment animals were placed in the trough of phenol red and as one moved about a single drop of one per cent NaOH was placed in its path. When the alkali was encountered the animal promptly stopped, made several random motions with its head and then moved off to right or left, thus giving a distinct avoiding reaction. The experiment was repeated using one per cent HCl instead of the alkali. To the acid the animals also gave a distinct avoiding reaction. On contact with the acid the pharynges

were extruded and when this occurred the animals were promptly removed to clear water to avoid injury.

P. fluviatilis, when placed in the trough similarly do not dispose themselves with reference to the H ion concentration; also similarly they avoid one per cent NaOH and one per cent HCl. *F. gracilis* enter either the acid or alkali ends of the trough but when allowed to stand for an hour or longer they accumulate toward the alkali end. The results were not decisive, however, for there were variations in different tests. *F. gracilis* react negatively to one per cent NaOH and to one per cent HCl.

REACTION TO TEMPERATURE CHANGES

According to my records and to reliable accounts, the cave water in which *S. percaeca* were collected has a temperature range of 12° to 14° C. My animals were kept in a constant temperature bath in glass containers at 15° C., plus or minus ½ degree F., for about two months without apparent ill effect.

When placed in a trough in water at 14° C. one centimeter deep and in their creeping they encounter a stream of water at 55° C. from the mouth of a pipette they give a slight avoiding reaction. In such a trough I used a cold pencil consisting of a narrow thin-walled test tube filled with melting ice, placing the pencil squarely in the paths of creeping animals. There were no indications of avoidance or other effect as the animals made contact with the glass, except that elicited whenever an obstacle of any sort was encountered. The animals crept under the end of the tube and in some cases climbed its wall. When the experiment was repeated using a test tube containing water at 55° C. there was a slight avoiding reaction in some cases; in general, the animals did not creep directly under the pencil but gave a trace of clearance as they proceeded.

Tolerance experiments could not be exhaustively tried due to danger of loss of my scanty stock, but two animals were on one occasion kept in water at 24° C. for three hours without injurious effect. The general conclusion reached was that, although in their native habitat the temperature is fairly constant, they tolerate temperature changes quite well and give avoiding reactions only when the temperature is elevated considerably above the physiological range of temperature tolerance of surface living flatworms.

The responses of *F. gracilis* and of *P. fluviatilis* to temperature differences were not tried. Incidental observations on stocks that have been handled in the laboratory over some years of experience indicate that both species are not sensitive to temperature ranges within the variations of room temperature and higher. The interesting fact is that *S. percaeca*, normally living in a constant comparatively low temperature, is similarly insensitive to temperature changes and exhibits tolerance to temperatures ten degrees above that of their environment.

REACTION TO LIGHT

The fact that *S. percaeca* is eyeless¹ does not preclude the possibility of light sensitivity. Eigenmann ('08) found two cave animals, *Cambarus pel-lucidus* and *Amblyopsis speleus*, to respond to light. But close observation of the cave flatworms on exposure to the diffuse light of a darkened room failed to reveal any agitation, nor are they stimulated in any way by the light from a Mazda bulb at nine and a half foot candles. They were then subjected to more vigorous tests. Four animals were placed in each of two test tubes in cave water at 17° C., pH 7.6, and shaken to the bottoms of the tubes. The upper half of one tube was covered with black paper. Both tubes were exposed to sunlight of 4000 foot candles intensity² for thirty seconds. The animals writhed violently in both tubes but those in the half covered tube made no attempt to seek the darkened end nor to escape. The tubes were then removed and the animals arranged in the middle of the tubes. The ends of the tubes were then covered with black paper and the tubes exposed to sunlight for one minute. One or more animals crept into the darkened ends of the tube but left again and none showed any preference for the dark region. The animals were then shaken to the bottoms of the tubes and that region covered with black paper. By this time the animals were becoming sluggish; two crept out of the darkened region but the remainder did not move about. It was presently noted that two of the animals were in the first stages of disintegration. They were all removed to the cold bath and within twelve hours six of the eight experimental animals had disintegrated. The total exposure to sunlight had been somewhat less than two minutes. Increase of water temperature in the test tubes probably was a factor in the injurious effect of exposure to sunlight; however, in the dark the animals tolerate distinctly higher temperatures, so the higher test tube temperature alone does not account for the injurious effect of the sunlight exposure.

In another experiment performed in the light of an east window on a cloudy afternoon four animals were placed in a test tube in cave water and the tube immersed in a glass dish which was placed over a background consisting of black and white paper. The test tube was so arranged that the animals in creeping within the tube would have to pass over the sharp margin of the black and white background. They were then examined continuously under a binocular. There was no indication whatever that the animals were in any way sensitive to the change in background as they passed from white to black and from black to white.

In more than two months observation of the cave forms exposed to light of different intensities, either diffuse daylight or light from electric bulbs, no indications were observed of any orientation or response to light in any

¹ The cave planarian described by Walter as light sensitive (Walter, H. E. 1907. *Jour. Exp. Zool.* 5) is apparently not *S. percaeca*. It is described as having eyes and was collected from Donaldson's Cave, Indiana.

way, except as noted above, namely, their writhing when exposed to direct sunlight.

REACTION TO FOOD

Although Banta ('07) and Scott ('09) have attempted diagrammatic representations of the food chain in cave animals, the information at hand is quite incomplete. In Mammoth Cave, *S. percaeca* is found together with several varieties of Crustaceae, particularly *Caecidotia stygia* (Packard) and *Crangonyx vitreus* (Cope). Kofoed ('99) has shown that the Echo River in the cave contains plankton. Since epigeal triclads feed freely on injured and moribund animals of various sorts, the assumption was made that *S. percaeca* normally feeds on animal tissues and juices. Absolutely no success was attained in inducing the animals to feed; otherwise it would have been possible to maintain a culture in the laboratory for more complete analyses of their behavior. *S. percaeca* were placed after one to three weeks starvation in both large and small quantities of water with the following materials: fresh beef liver; crushed earthworm; crushed and living land isopods; crushed and living cave isopods; crushed *E. dorotocephala*; tissues of a newt; fish food containing shredded shrimp and egg powder; Cladocera; black garden soil; partially decayed leaf; bread mold; pleurococcus. In no case was the pharynx extruded nor any reaction observed that could be interpreted as a response toward or away from the food. When placed directly upon a piece of beef liver, for instance, their behavior was identical with that observed when they were placed on a piece of broken glass.

The fact that *S. percaeca* occurs together with cave isopods strongly suggests that they feed in part at least on these animals, but my attempts to confirm this in the laboratory were failures. In April a small piece of meat was cached near the stream in Annette's Dome and in November it was recovered in the water nearby. Within two inches of it two *S. percaeca* were found. But more complete studies of the animals in their native habitat must be made before a definite statement concerning their food relations can be made.³

REGENERATION

Failure to find a food for the animals restricted experimentation upon their regenerative characteristics to five animals. One animal was cut to remove the head and the remainder into approximate halves, the pieces being placed in small flasks and immersed in cold water. Two weeks later the head showed what was thought to be signs of disintegration. The wound had healed and the integument was expanded to form a thin-walled vesicle. There was no external indication of posterior regeneration. Ten days later the conditions had not changed, but when examined six weeks after cutting, the head piece had regenerated a complete small animal, the vesicular structure

³ Certain aspects of the activities and inter-relations of cave animals are now being investigated in this laboratory.

having undergone reorganization. I have never observed regeneration to occur with the formation of a vesicle in *Euplanaria* nor in *Fondicola* or *Procotyla* but Coe ('29) records the formation of vesicles in abortive regenerative processes in a nemertean.

The anterior half of the animal regenerated a complete animal; the initiation of head regeneration was observed one week after section. Regeneration was complete within six weeks, the regenerate being at this time normal as to form and about 2.5 mm. in length. The posterior half of the animal also regenerated but much more slowly than the anterior. The first indications of a head did not appear until two weeks after section. Six weeks after section the form was almost normal and about 3.5 mm. long.

Another small animal was cut into thirds. The head died as did also the anterior and middle thirds. The posterior third healed the wound but did not proceed further with regeneration. Another eight millimeter animal was cut in two to include approximately the anterior third including the head in one piece and the posterior two-thirds in the other. Both pieces regenerated completely within six weeks. In the posterior pieces the head was distinctly smaller than normal at this time. In another case the regeneration of a posterior half was followed to complete regeneration and that of a posterior third showed no regeneration. In no case was there any external indication of eye formation. From these incomplete experiments it may be concluded that regeneration rate decreases as pieces are taken from more posterior levels, that pieces anterior to the mid-region are capable of regeneration, and that if the level of section is in the posterior half of the animal, regeneration may not occur. In this respect *S. percaeca* more closely resembles *P. fluviatilis* than *F. gracilis*. In the former, according to Lillie ('01) regenerative capacity is limited to the region anterior to the pharynx, an observation confirmed by Sivickis ('31) and frequently observed by the writer in unpublished work. In *F. gracilis*, extreme posterior one-eighth pieces regenerate in four per cent of cases; regeneration of the posterior one-third occurs in eighty-six per cent of cases (Buchanan, '33).

REACTION TO HYPOTONICITY

Two *S. percaeca* were placed in distilled water for observation. After several hours it was noted that they were somewhat less active than normal but after an exposure of twenty-four hours there was no indication of cytolysis or other injury.

REACTION TO METHYLENE BLUE AND TO POTASSIUM CYANIDE

S. percaeca placed in one-half per cent reduced methylene blue did not absorb the dye during a fifteen minute exposure. The solution was much too toxic to continue the treatment; a sufficient number of animals to determine an appropriate concentration for further study was not at hand. After forty

minutes in one-half per cent oxidized methylene blue the dorsal surface was heavily stained, slightly more intensely anteriorly than posteriorly. The ventral surface stained lightly but more heavily anteriorly than posteriorly. The line of demarkation between the dorsal and ventral surfaces was sharply set forth by the marked differences in intensity of staining. During the last stage of exposure to the dye and after removal to tap water the ventral region swelled, causing the animals to assume a crescentic shape with the dorsal surface inward. One hour after removal from the dye the anterior ends began to disintegrate; the body wall opened and white opaque materials disseminated. Disintegration proceeded slowly posteriorly; slow waves of muscular contraction swept from anterior toward posterior. In two hours the disintegration had reached the middle of the long axis and in two and a half hours it reached the vicinity of the pharyngeal sheath. The posterior end then rapidly disintegrated.

In one experiment two animals were placed in M/1500 alkaline KCN made up in tap water and in another two were placed in M/2500 KCN. In both disintegration was complete in less than three hours. While it appeared that the anterior ends were first affected, the process of disintegration was too rapid to enable one to detect material differences in rate in different regions of the animals.

From the observations on the disintegrative action of methylene blue and from the data on rate and occurrence of regeneration, it seems quite probable that the cave triclad is characterized by an antero-posterior physiological gradient. In this they resemble the epigeal triclads. Evidently this physiological pattern is not materially altered by reason of their age-long tolerance of a habitat that is totally free from the functional responses induced by light and by temperature change.

SUMMARY

A study of forty living specimens of an American cave triclad, *Sphalloplana percaeca* (Packard), permits the following tentative conclusions:

The animal does not orient to light but writhes violently and may be killed by a two-minute exposure to sunlight. There is no evidence of orientation to gravity in air-saturated water, in water with low oxygen tension, in foul water, nor under water pressures up to twenty pounds per square inch. Water currents and the passage of water films over its surface agitate the animal but there is no orientation. It appears indifferent to hydrogen ion concentrations between pH 6.6 and pH 8.0, but shows a sharp avoiding reaction to one per cent HCl and to one per cent NaOH. It exhibits no orientation to temperatures between approximately 4° C. and 55° C. and tolerates temperatures up to 24° C. for at least three hours. The animal is highly susceptible to KCN, much less so to a hypotonic environment. When colored with methylene blue there are indications of an antero-posterior color gradient. When disintegrating after treatment with methylene blue a disintegration gradient is detectable.

Cross pieces taken from the anterior half of the animal regenerate new individuals. The processes of regeneration are slower the more posterior the level of origin of the piece. It is probable that pieces taken from the posterior half of the animal do not regenerate.

Comparable observations on the epigeal triclads *Procotyla fluviatilis* and *Fondicola gracilis* and to a lesser extent on *Euplanaria dorotocephala* and *Euplanaria maculata* have been made. *Sphalloplana percaeca* was first assigned to the genus *Dendrocoelum* by Packard but recently has been transferred to the Planariidae and by one investigator to the genus *Fondicola*. Incomplete evidence is submitted here that in its reactions it more closely resembles *P. fluviatilis*, a member of the Dendrocoelidae, than the Planariidae, *F. gracilis*, *E. dorotocephala*, and *E. maculata*.

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RAINFALL RECORDS FOR THE SONORAN DESERT. II. SUMMARY OF READINGS TO DECEMBER, 1935¹

T. D. MALLERY

Desert Laboratory, Tucson, Arizona

Additional semi-annual readings have been obtained which make it possible to give complete data for the rainfall for the Sonoran Desert to December, 1935. Numerous requests for this information and manifest interest in the rainfall of this region have furnished the incentive for making the data available and for keeping them up-to-date.

Table I consists of a tabulation of the average precipitation records ob-

TABLE I. *Long-period raingauge readings for the Sonoran Desert to December, 1935. The figures in parentheses indicate the number of readings upon which the average is based*

Station	Elev. in ft.	Date estab.	Average precipitation in inches		
			Summer	Winter	Annual
<i>Libertad Series</i>					
1. Cirio Point	180	April '25	2.41 (9)	1.57 (8)	4.08 (10)
2. Puerto Libertad	100	April '25	2.31 (9)	1.66 (8)	4.68 (9)
3. 19 Mi. Pass	1620	April '25	8.20 (8)	2.48 (8)	10.68 (8)
4. 50 Mi. Pass	1400	April '25	10.06 (9)	1.76 (8)	12.08 (9)
5. Las Temporales	1100	April '25	5.94 (3)	0.93 (2)	10.87 (3)
6. Oquitoa	1700	Oct. '32	5.68 (2)	2.13 (2)	7.82 (2)
7. Red Rock Crossing	1700	April '32	9.65 (4)	2.94 (3)	13.26 (3)
8. Los Molinos	2340	April '32	7.75 (3)	4.78 (2)	12.40 (2)
9. Baboquivari	3675	April '31	13.30 (4)	5.96 (3)	17.98 (4)
<i>Local Series</i>					
10. Sierrita Mts.	4100	May '28	10.94 (7)	4.94 (6)	16.45 (7)
11. Avra Valley	2400	Nov. '26	6.65 (6)	3.46 (6)	10.11 (6)
12. Soldier Camp	7875	May '26	18.51 (10)	16.22 (7)	33.45 (7)
13. Pima Canyon	2600	May '30	8.47 (5)	4.75 (4)	11.00 (5)
14. Desert Laboratory grounds	2500				
A. Near N. gate		April '26	7.95 (9)	3.99 (7)	10.91 (7)
B. Midway between N. & S. boundaries		May '28	6.50 (6)	4.87 (5)	12.72 (7)
C. N. W. corner		June '30	5.77 (5)	5.20 (4)	13.17 (5)
D. S. W. "		June '30	5.85 (5)	4.70 (4)	12.39 (5)
E. S. of Tumamoc Hill		June '30	6.24 (5)	4.77 (4)	13.20 (5)
F. Summit of Tumamoc Hill	3100	Nov. '26	7.57 (8)	4.21 (8)	10.78 (9)
<i>Camino del Diablo Series</i>					
15. Sells	2500	Mar. '32	7.71 (3)	3.91 (3)	11.62 (3)
16. 23 Mile Hill	2350	Jan. '29	7.13 (4)	4.05 (3)	11.26 (6)
17. Growler Pass	1400	Mar. '32	4.37 (4)	4.39 (3)	8.27 (3)
18. Agua Dulce	1140	Oct. '26	3.72 (6)	3.66 (6)	6.98 (9)
19. Pinacate Plateau	910	May '28	3.35 (5)	2.76 (4)	4.25 (7)
20. Tule Tank	1115	June '26	2.38 (7)	1.94 (6)	4.13 (8)
21. Tinajas Altas	1050	June '26	2.45 (7)	2.83 (6)	5.47 (8)
22. Lechuguilla Desert	715	Oct. '32	1.26 (3)	3.06 (3)	4.32 (3)

¹ The excess of tabular material in this article is made possible by funds other than those of the Ecological Society of America.

tained to date for the various raingauge stations. The numbers preceding the names of the stations correspond to the number used in the descriptions of the stations and their locations on the map in the earlier publication by Mallery.¹

The graph, figure 1, shows the relation of the average amount of winter

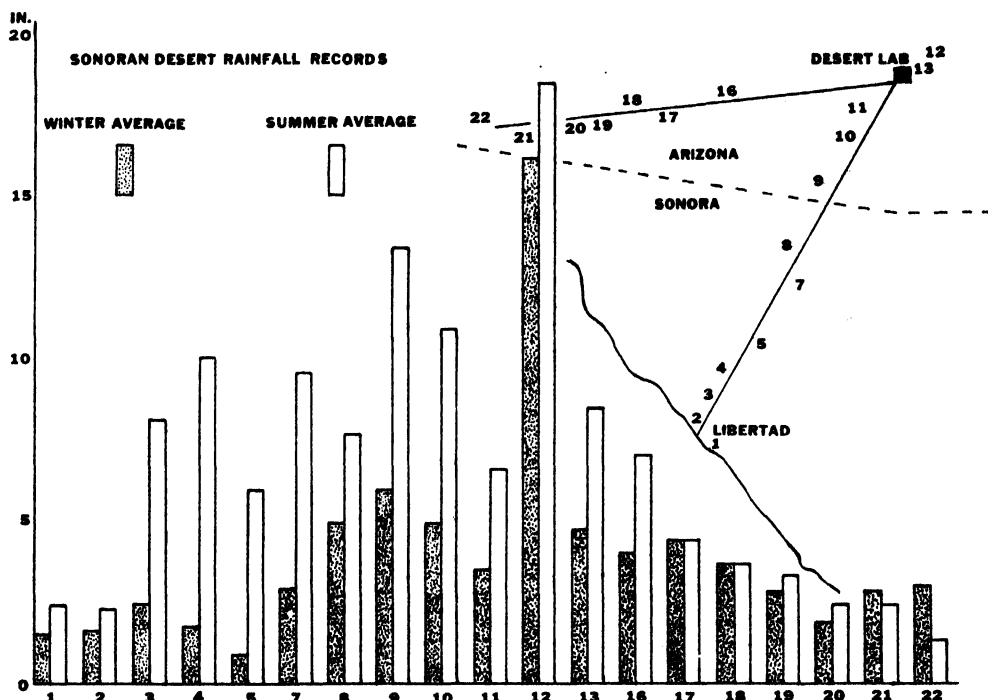


FIG. 1. A comparison of the average winter and summer rainfall records for long-period raingauge stations on the Sonoran Desert. The relative location of the stations is shown diagrammatically in the upper right-hand portion of the graph.

rainfall, represented by the left-hand column in each case, to the average summer rainfall, represented by the right-hand column, for the respective stations which are representative of the entire group. It is not known what effect the presence of nearby peaks, the pitch of the slope, or the height of land mass immediately above a gauge station may exert upon the rainfall. These factors also are being investigated at the Desert Laboratory.

At most stations it may be noted that the summer rains are greater in amount than the winter rains. As one goes westward, however, they tend to become more nearly equal in amount and in the extreme southwestern corner of Arizona the winter rains are greater in quantity than the summer rains. Unpublished analyses of data from 118 Weather Bureau Stations in Arizona by Glenton Sykes of the U. S. Forest Service show that in most

¹ Mallery, T. D. 1936. Rainfall records for the Sonoran Desert. *Ecology* 17: 110-121. 2 fig.

sections of the state the winter rains are greater and that only in southeastern and southcentral Arizona, and two relatively small areas in east-central and northeastern Arizona are the summer rains greater in amount than the winter rains. The long-period raingauge readings reported in this paper coincide with these analyses so far as the areas covered overlap.

In lieu of more detailed rainfall distribution data the maximum and the minimum summer and winter raingauge readings are given in table II for

TABLE II. *Seasonal range and seasonal average of long-period raingauge readings for the Sonoran Desert from date of establishment of the respective stations to December, 1935. The ratios of minimum to maximum readings and of winter to summer averages are also shown*

Station	Seasonal range						Seasonal average		
	Summer			Winter			Summer	Winter	Ratio (Summer = 100)
	Max.	Min.	Ratio (Max. = 100)	Max.	Min.	Ratio (Max. = 100)			
	<i>in.</i>	<i>in.</i>		<i>in.</i>	<i>in.</i>		<i>in.</i>	<i>in.</i>	
1. Cirio Point.....	11.17	0.43	3.8	2.90	0.27	9.3	2.41	1.57	65.1
2. Puerto Libertad.....	8.93	0.62	6.9	4.00	0.39	9.7	2.31	1.66	72.0
3. 19 Mi. Pass.....	14.48	4.14	28.6	4.73	0.48	10.1	8.20	2.48	30.2
4. 50 Mi. Pass.....	19.64	4.39	22.3	3.62	0.62	17.1	10.06	1.76	16.6
5. Las Temporaes.....	8.39	4.24	50.3	1.20	0.67	55.8	5.94	0.93	15.6
6. Oquitoa.....	6.46	4.91	76.0	3.80	0.47	12.4	5.68	2.13	37.5
7. Red Rock Crossing.....	14.46	6.42	44.4	4.22	0.85	20.1	9.65	2.94	30.5
8. Los Molinos.....	8.01	7.58	94.5	5.77	3.80	65.4	7.75	4.78	61.3
9. Baboquivari.....	16.21	8.66	53.2	9.05	3.53	39.0	13.30	5.96	44.8
10. Sierrita Mts.....	23.75	3.75	15.8	7.32	1.83	25.0	10.94	4.94	45.2
11. Avra Valley.....	11.61	2.68	23.1	5.95	1.85	31.3	6.65	3.46	52.0
12. Soldier Camp.....	29.82	9.82	32.9	24.64	4.27	17.3	18.51	16.22	87.3
13. Pima Canyon.....	14.28	3.36	23.5	9.00	1.25	13.9	8.47	4.75	56.1
14. Desert Lab. grounds									
A. Near N. gate.....	14.73	4.04	27.4	7.33	1.46	19.8	7.95	3.99	50.2
B. Midway between N. & S. limits.....	9.28	4.46	48.1	7.93	1.64	20.7	6.50	4.87	74.9
C. N. W. corner.....	8.12	3.87	47.7	8.20	1.85	22.6	5.77	5.20	90.2
D. S. W. corner.....	8.20	3.62	44.2	7.37	1.81	24.6	5.85	4.70	80.4
E. S. of Tumamoc Hill.	9.50	3.72	39.1	7.40	1.77	23.9	6.24	4.77	75.8
F. Summit of Tumamoc Hill.....	13.66	3.23	23.6	7.93	1.56	19.7	7.57	4.21	55.6
15. Sells.....	12.07	5.27	43.6	4.90	2.93	59.8	7.71	3.91	50.7
16. 23 Mile Hill.....	10.53	3.88	36.8	5.35	2.15	40.2	7.13	4.05	56.4
17. Growler Pass.....	5.86	2.80	47.8	6.78	1.51	22.3	4.37	4.39	100.4
18. Agua Dulce.....	6.79	2.15	31.7	6.40	1.29	20.1	3.72	3.66	98.7
19. Pinacate Plateau.....	7.00	0.89	12.7	6.25	0.13	2.8	3.35	2.76	82.4
20. Tule Tank.....	6.43	0.00	0.0	4.22	0.00	0.0	2.38	1.94	81.5
21. Tinajas Altas.....	5.08	0.31	6.1	4.50	1.25	27.8	2.45	2.83	115.5
22. Lechuguilla Desert.....	2.41	0.36	14.9	4.22	0.95	22.5	1.26	3.06	242.9

each station. The spread between the highest and lowest readings is designated as the range of seasonal precipitation. The range therefore indicates the extreme conditions, to which the plants have become adjusted, so far as

amount of rainfall is concerned. The seasonal averages are repeated in this table to facilitate comparisons and the ratios of the minimum to the maximum readings and of the winter to the summer averages are also included.

At those stations where the ratio values for the maximum and minimum readings more nearly approach 100, there is apparently more certainty that the seasonal precipitation will not depart greatly from the average amount. It is apparent, however, that these ratio values are subject to the direct influence of unusual seasons and storms. For example, the summer maximum readings for stations 1 and 2 are very high as compared with the usual amounts and both of these readings were obtained for the summer rains of 1926. These unusually high readings were in all probability due to a single heavy rain. This phenomenon has been experienced numerous times in this desert region and attests again to the extreme localized distribution and uncertain quantity of the seasonal rainfall. While stations 1 and 2 are only 6 miles apart and are in very similar situations yet there was over 2 inches more rainfall at station 1 during the summer of 1926. It is interesting to note also that station 12 at an elevation of 7875 feet in the Santa Catalina Mountains has a greater range in the amounts of summer and winter rainfall than do many of the stations at much lower elevations on the desert plain.

In general the amounts of summer rains at most of the stations are less variable from year to year than are the winter rains. Stations nearest the Gulf of California tend to have a more dependable rainfall in winter than in summer.

It is planned to continue the long-period raingauge study of the Sonoran Desert for another period of years.

OXYGEN CONSUMPTION IN FRESH WATER FISHES¹

RALPH G. CLAUSEN

N. Y. State College for Teachers, Albany, N. Y.

The amount of oxygen that is consumed by an animal is considered as a valid standard of its metabolism. It has been generally accepted as a scale to measure the energy that is being expended by the animal. The consumption of oxygen by fresh water fishes has had its share of investigation, but most of the work has been done with the purpose of determining the total amount of oxygen consumed over a period of time. In this type of study the initial oxygen concentration and the final oxygen concentration are compared, but we have little information on what happens between the two determinations. So far as I am informed, no one has attempted to take relatively continuous determinations of the oxygen consumption. This paper is a report on a series of experiments that had for their purpose the determination of the oxygen consumption of certain fresh water fishes during 24 hour periods.

APPARATUS FOR THE DETERMINATION OF THE OXYGEN CONSUMPTION

Almost no work has been done with running water in the determination of the oxygen consumption of a fish. In order to take samples at will, it is necessary that there be a constant supply of water given to the fish and an equal amount taken away. This can be done only in an apparatus which will furnish a constant flow of water.

The apparatus (fig. 1) used in these experiments was suggested by one described by Keyes ('31) (also see Schuett, '33). Its principal parts were three No. 1 lamp chimneys (*A*, *B*, *C*). The water was led from an aerator into an inverted Woulff bottle (*D*) which was used as a reservoir and maintained a constant pressure by means of an overflow pipe. From the reservoir the water passed into another Woulff bottle (*E*) where the temperature was taken with a thermometer calibrated to 0.1° C. The points of three thermocouples (1, 2, 3) were attached to the bulb of the thermometer. The second Woulff bottle was immersed in water to keep its temperature more constant. The water then passed through a four-way joint (*K*), and was distributed through glass stop-cocks to the three experimental chambers (*A*, *B*, *C*) and to the control bottle (*H*). The water was allowed to flow out of the chambers through glass T tubes into which were placed the other points of the thermocouples (1', 2', 3'). In this way it was possible to obtain comparative

¹ Contribution from the Zoological Laboratory of the University of Illinois, No. 479.

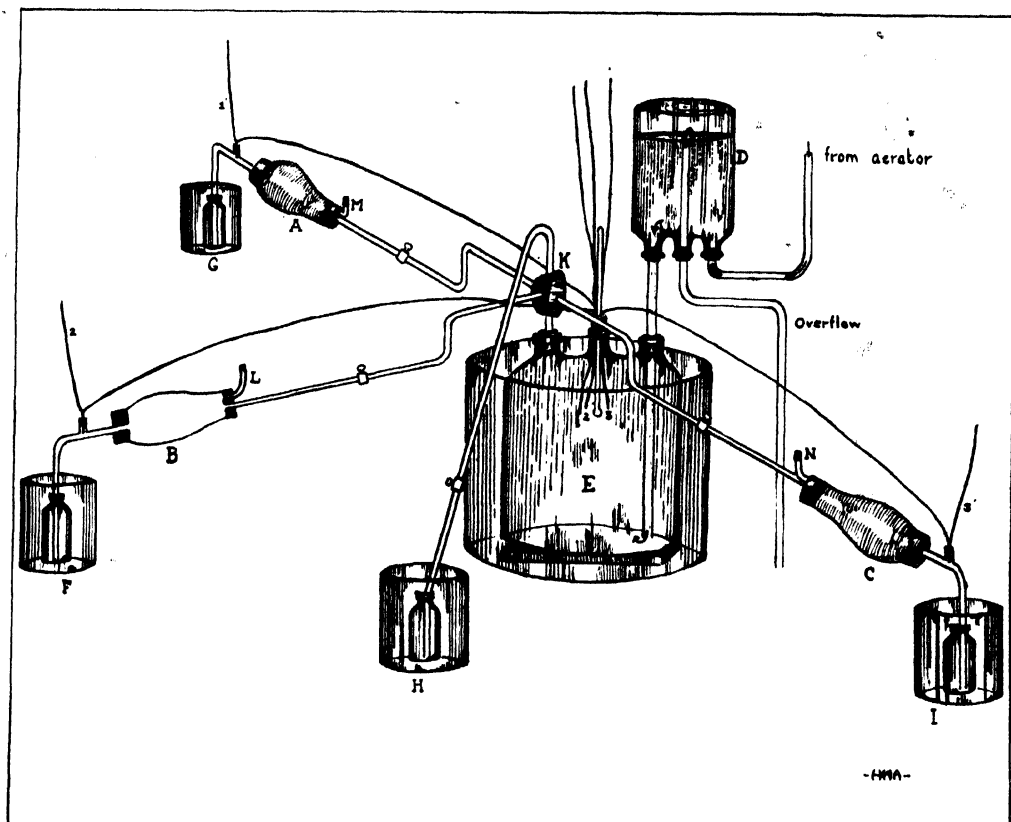


FIG. 1. The Apparatus for the determination of Oxygen Consumption.

temperatures of the water without the necessity of calibrating four thermometers. Tubes (*L*, *M*, *N*) were introduced into the experimental chambers so that any air bubbles in the experimental chambers could be removed without disturbing the fish. These tubes were necessary in filling the chambers after the fishes were introduced. During the period of actual experimentation these tubes were securely stoppered. The samples were collected in bottles placed in battery jars (*F*, *G*, *H*, *I*).

PROCEDURE FOR THE DETERMINATION OF OXYGEN CONSUMPTION

The apparatus was set up and allowed to remain unchanged as long as possible. This was done in order that the supply of water passing through the aerator would be as constant as possible during the time of experimentation.

The fishes were introduced into the experimental chambers at least twelve hours before the experiment was begun. Inasmuch as the body temperature of the fish is increased by stimulation (Clausen, '34), the experimental chambers were covered so that any external movement could not act as a stimulus.

The covering was a cloth wrapped around the chambers. It was necessary that this covering be loose enough around the upper end of the chamber to allow an inspection for air bubbles without uncovering the entire chamber.

The samples were collected every hour for twenty-four hours. The tubes from the chambers and the control tube were placed in the collecting bottles, reaching to the bottom of the bottles, and the water flowed into the bottle for forty-five minutes. This permitted more than ten times the capacity of the bottles to flow into and out of the bottles. The overflow from the bottles was caught in battery jars in which the collecting bottles were placed, so that at the end of the forty-five minutes the collecting bottles were completely submerged and the glass stoppers were in place before the bottles were removed.

The oxygen was determined by the regular Winkler method² according to the Birge and Juday formula ('11). Approximately N/100 thiosulphate was used in the titrations. This was standardized against N/100 potassium bichromate, and the same stock solution of bichromate was used throughout the entire series of experiments. The water used was a hard water from deep wells, received in a storage tank, chlorinated, sand filtered, and stored in a second tank. When it reached the tap it contained little oxygen, and 0.3 to 0.5 parts per million chlorine. The water was run over a crimped metal aerating device which reduced the chlorine to 0.03 to 0.04 p.p.m. which is about 0.1 the lethal concentration for the most sensitive fishes used. At the same time the oxygen was raised to between three and six parts per million. The water was below the oxygen saturation point but was not below the "biological minimum." It has been generally understood that the nitrates are oxidized in water treated with chlorine. After this work was completed some variability of the readings with orthotolidene led to a series of determinations of nitrate in water treated in the same way, by Mr. F. L. Coventry. It was found to contain 0.2 p.p.m. with a variation from day to day of only about 0.01 either side of the mean (Coventry, Shelford, & Miller, '35). The uniformity of the amount present and the uniformity of treatment by one operator probably made only a slight difference. The Rideal-Stewart modification was not used largely because it rendered hourly determinations impracticable.

The temperature of the water was closely controlled. All the experiments were done at temperatures between 17° and 20° Centigrade, and in no individual experiment did the temperature of the experimental water vary more than one degree during the twenty-four hours of the experimental period.

The water was allowed to flow through the experimental chambers by way of glass stop-cocks. The standard rate of flow was taken to be fifty cubic centimeters per minute. It was impossible to maintain this flow constantly, but before and after each sample was taken the flow was checked with

² The experimental work of this report was completed before the appearance of Allee & Oesting's Critique of the Winkler method ('34).

a stop-watch. This check was made by allowing the water from each experimental chamber and the control tube to fill a one hundred cubic centimeter bottle. The maximum variation allowed was six seconds in the two minutes which were required to fill the bottle.

In order to further lessen this source of error each sample was corrected by standardizing the amount of oxygen in the sample to a flow of fifty cubic centimeters per minute. The correction is based upon the assumption that the amount of oxygen in the sample was proportional to the flow. The amount of water that passed through the apparatus was not enough to operate the aerator at its maximum efficiency, so that any increase in the flow of water resulted in more efficient aeration. This correction is not perfect and varies with the size of the fish, but the results are more nearly correct than they would be if no correction were used.

The corrected amount of oxygen in the samples was then subtracted from the amount of oxygen in the control sample, and the amount of oxygen consumed by the fish was ascertained.

Inasmuch as the consumption of oxygen by an animal is a continuous function, the time when the samples are taken is an arbitrary thing. In these experiments hourly samples were taken and the titrations were performed while the subsequent sample was being taken. This procedure necessitated two sets of sample bottles. In order to compensate for the difference in bottles and also to diminish any error in a single determination, the average of two consecutive samples is used in the data. In making this average, however, some of the characteristic variations are lost, and the curves are too smooth.

FISHES USED IN THE EXPERIMENTS

The fishes used in these experiments were taken from the streams and ponds of Champaign County, Illinois. They were kept in tanks until they were used. All of them had been starved for some time before they were introduced into the experimental chambers.

The fishes used were: Greensided darter (*Etheostoma blennioides* (Raf.)), Stone roller (*Campostoma anomalum* (Raf.)), Chub sucker (*Erimyzon sucetta oblongus* Mitchill), Common shiner (*Luxilus cornutus* (Mitchill)), Golden shiner (*Notemigonus crysoleucas* (Mitchill)), White crappie (*Pomoxis annularis* Raf.), Black bullhead (*Ameiurus melas* (Raf.)), Largemouth Black Bass (*Huro salmoides* (Lacépède)).

The habitat relationships of these fishes have been worked out by Thompson and Hunt ('30). According to this study the darter is found in the swiftest riffles of rocky rapids; the stone roller is found most abundantly in "gravelly and sandy riffles and stretches," the chub sucker haunts many habitats, but is listed primarily in "vernal rivulets"; the shiners, golden and common, inhabit "stretches of shallow, sluggish water" abundantly; the bullhead

is found in "oxbow ponds along small streams"; the white crappie and the largemouth bass live in "moderately deep smoothly flowing stretches."

RESULTS

The data of these experiments may be viewed from many angles and may be handled in different ways. It will serve the present purpose to merely tabulate the results, and then point out two inferences that may be drawn from the table.

Table I summarizes all the data of the entire series of experiments. Column 1 lists the fishes that were used in the experiments. They were chosen for this study because of their known ecological differences. Column 2 gives the weight of each fish in grams. Column 3 gives the date when the fish was in the experimental chamber. It will be noticed that, except black bass No. 2, No. 3, No. 4; white crappie No. 2 and No. 3; and common shiner No. 2 and No. 3, two members of the same species were not tested on the same day. Column 4 gives the temperature of the water during the period of experimentation. Column 5 is the oxygen consumption of the fishes in parts of oxygen per million parts of water. The column is divided into two parts. The first part is the two-hourly average of the oxygen consumption of the individual fishes. The second part of column 5 gives the total amount of oxygen that was consumed by each fish during the experiment. Column 6 gives the amount of oxygen in parts per million parts of water that was consumed by each gram of fish during the twenty-four hours of the experiment. This figure is obtained by dividing the total oxygen consumption (part two of column 5) by the weight of the fish (column 2). In column 7 the daily oxygen consumption per gram of fish (column 6) is averaged for each species.

It is also possible to calculate the oxygen consumption in milligrams per kilogram of fish per hour. Inasmuch as the water went through the experimental chamber at a rate of 50 cc. per minute, in an hour 3000 cc. would go through. A fish that reduces the incoming water one part per million (by

TABLE II. *Oxygen consumption of fish in milligrams per kilogram and per surface units*

Kind of fish	Number of determinations	Mgm. Oxygen consumed per kilo per hour		Mgm. Oxygen consumed per 100 surface units per hour	
		Mean	Probable error of mean	Mean	Probable error of mean
Black Bass	48	65	±2.3	228	±8.2
Black Bullhead	36	73	±1.9	273	±7.2
White Crappie	36	91	±6.0	205	±13.4
Golden Shiner	36	97	±6.1	278	±17.4
Common Shiner	41	131	±7.1	329	±17.9
Chub Sucker	30	153	±7.5	449	±19.0
Stone Roller	24	187	±7.7	500	±20.5
Green-sided Darter	24	210	±10.8	261	±13.5

weight) per hour will be using $1/1,000,000 \times 3000$ grams (cc. of water), or 3 milligrams of oxygen per hour. A fish reducing the oxygen concentration 1 part per million per hour will be using oxygen at the rate of $3 \times 1000/W$ milligrams per kilo of fish per hour. W is the weight of the fish in grams. Therefore the amount of oxygen consumed, in parts per million (by weight) per hour, multiplied by 3000 and divided by the weight of the fish in grams, is the rate of oxygen consumption in milligrams per kilo of fish (Krogh, '15). If the oxygen consumption is to be figured according to surface units the formula may be changed to $3 \times 1/\sqrt[3]{W^2}$. Table II is a compilation of the data according to these formulae (Rubner, '24).

DISCUSSION

(1) From the data of these experiments it is apparent that the rate of oxygen consumption in fresh water fishes is not a constant, steady function. It varies in the same fish from hour to hour, and shows differences between individuals of the same species. This seems no more than natural to one who is acquainted with these animals in their native environment. They are rarely active for extended periods of time, nor do they remain quiescent for long. However, these fluctuations are not entirely haphazard, as a close examination of the data will show. In the case of the black bass (fig. 2), it

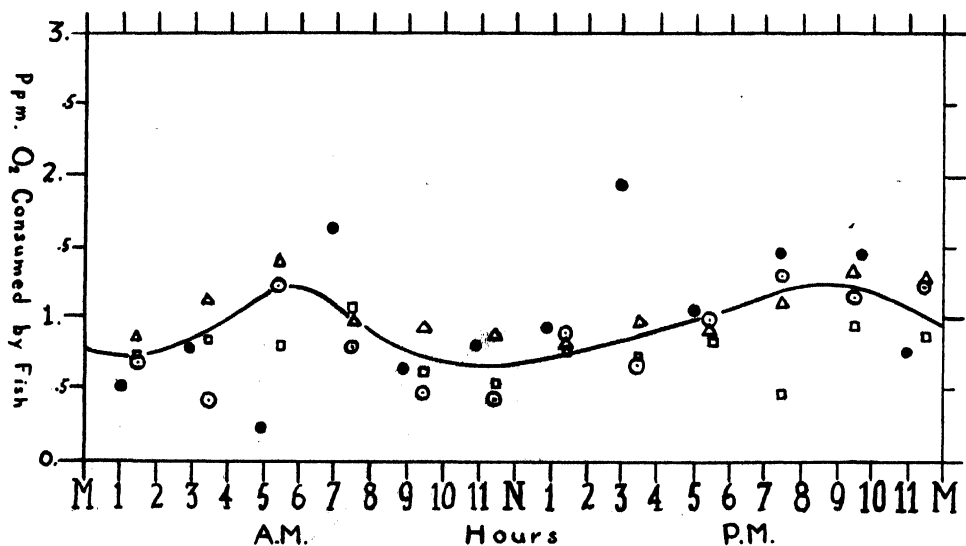


FIG. 2. Oxygen Consumption of Large Mouth Black Bass.

● Fish No. 1, ○ Fish No. 2, △ Fish No. 3, □ Fish No. 4.

will be noticed that all four fishes agree in having a low oxygen consumption between 9 A.M. and noon, while between 5 A.M. and 8 A.M., and again between 3 P.M. and 10 P.M., there is a time of relatively high consumption of oxygen. In the black bullhead most of the high points of oxygen consumption fall

during darkness, between 5 P.M. and 4 A.M., while during the daylight hours the amount of oxygen consumed is relatively low. In the unaveraged data for the black bullhead there appears a very characteristic irregularity in oxygen consumption between 5 P.M. and 10 P.M. This is seen in bullhead No. 2, but is lost in the averages for No. 1 and No. 3. The white crappie shows a relatively high oxygen consumption at 5 P.M., and a relatively low oxygen consumption during the morning hours, between 9 A.M. and 1 P.M. The golden shiner and the chub sucker are the only two species of fish in these experiments which show similar periods of high and low oxygen consumption. These two species have their high oxygen consumption during the middle of the day, but the high points do not coincide exactly.

The cause of these rhythmic fluctuations in oxygen consumption is not obvious. The constant environment of the experiments precludes any possibility of stimulation being the cause of these rhythmicities. If this were the case, it would be impossible to place three fishes of three different species in the experimental chambers at the same time and obtain three different rhythms. The rhythms of the bullhead, the crappie, and the common shiner have almost nothing in common, but they all gave characteristic readings when the oxygen consumption was taken during the same twenty-four hours (11:1:33), and the individual rhythms compare favorably with those of the other members of the respective species that were obtained at different dates. Nor is this rhythm easily broken. The black bullhead is probably the most sensitive to light of any of the fishes tested in these experiments. But the rhythm of bullhead No. 3 was obtained from a fish that was exposed to light, while the determination of bullhead No. 1 and No. 2 were done in covered experimental chambers. Although the total consumption of oxygen for bullhead No. 3 is low, its rhythm is quite the same as the rhythms of No. 1 and No. 2 (fig. 3).

The presence of oxygen consumption rhythms in fishes should not be unexpected. Recent investigations have shown that most animals have definite metabolic or activity rhythms (Carpenter, '35, Park, '35, Lutz, '34, Baldwin and Kendeigh, '32, Rau, '31, Johnson, '26, Wetmore, '21, Simpson and Galbraith, '05). Certainly there are activity rhythms in fishes, and these should be expressed in the metabolism of the animals.³

These daily fluctuations are probably a part of the larger rhythms which harmonize with the physiological cycles in the life history of the animal. Wells ('14) points out the difference in the resistance of fishes during the breeding season and later in the summer. This can not be due solely to the changes in the physical conditions of the environment. The tremendous changes that must take place in anadromous and other migrating fishes must be accompanied by changes in the metabolic rate, and should be discernible in the oxygen consumption of the fishes.

³ Mr. J. D. O'Donnell of the Illinois Natural History Survey using another method, has demonstrated activity rhythms in the largemouth black bass and in the black bullhead, that are in general agreement with the graphs shown in this paper.

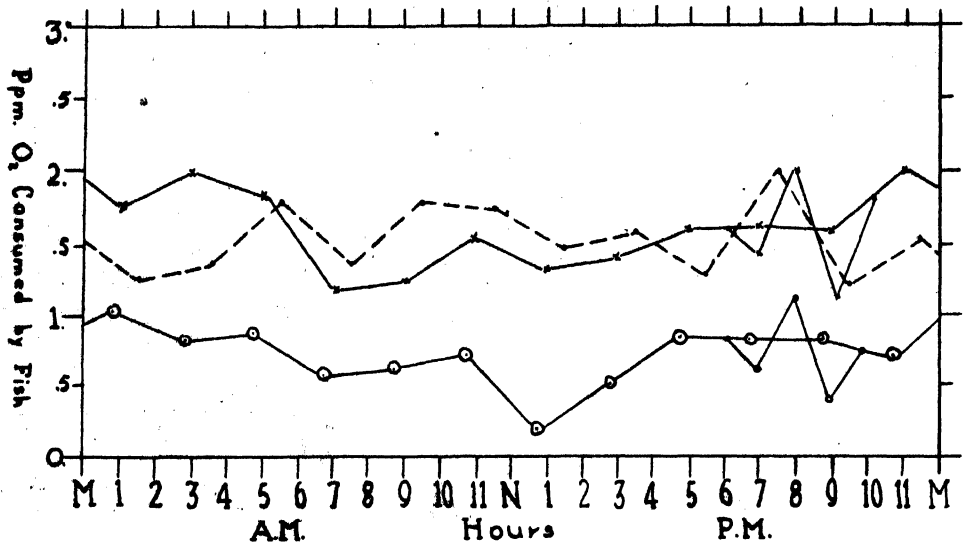


FIG. 3. Oxygen Consumption of Black Bullhead.

X—X Fish No. 1, ●—● Fish No. 2, ○—○ Fish No. 3.

In ecology, with further knowledge, the presence of these rhythms may become useful as an index to the time of activity and feeding of the fishes. In this way the rôle which the animal plays in the coactions of the community may be inferred. For instance, if periods of high oxygen consumption denote periods of activity, two fishes may live in the same habitat without a great deal of competition. The golden shiner and the black bullhead might live in the same pool and rarely meet in the struggle for existence. The activity periods of one correspond to the quiet periods of the other.

It is not the presence of oxygen consumption rhythms that is the most startling induction that can be drawn from these data, but the seeming lack of oxygen consumption rhythms in some of the fishes tested. No rhythms were evident in the determinations of the common shiner, the darter, or the stone roller, except a bare suggestion in the case of the stone roller. These fishes all live in the rapidly flowing water of a stream, and it may be that the lack of rhythm in oxygen consumption is characteristic of the inhabitants of fast flowing water.

(2) Shelford ('11) and Wright ('18) agree quite closely on the order of fish succession in a stream. Wright's order for the fishes used in these experiments is: common shiner, stone roller, golden shiner, black bullhead, black bass, chub sucker. He makes no report on the crappie and the darter. In Shelford's study the chub sucker appears earlier than in Wright's streams, and the common shiner comes in later. Shelford finds the crappie in the same pool as the bass, and Thompson and Hunt report them from the same habitat. The latter found the darters only in the swiftest water ('30).

If the fishes tested in these experiments are arranged in the order of the

average daily oxygen consumption per gram of fish for each species (table I, Column 7), it will be noticed that they assume almost precisely the reverse order of their successional sequence in a stream. The fishes which have their habitat in the relatively rapid waters consume more oxygen per unit of weight than the fishes which live in quiet waters. These results coincide with those of Fox and Simonds ('32) who found a similar relationship between the oxygen consumption and the habitat in aquatic insect larvae. In fishes this may be a function of relative size, but these two factors added to the factor of visual stimulus in rheotropism (Clausen, '31) can form a basis for a mores ratio of the longitudinal position of a fish in a stream.

SUMMARY

Hourly determinations of the oxygen consumption of eight species of fishes show that there are fluctuations in the amount of oxygen consumed by a fish. In the species which inhabit relatively quiet water (Largemouth black bass, black bullhead, white crappie, golden shiner, and chub sucker) the fluctuations tend to fall into a rhythm that is characteristic for each species. No definite rhythm was found in the oxygen consumption of the fishes (stone roller, common shiner, greensided darter) which inhabit rapid flowing water.

There seems to be a relationship between the amount of oxygen consumed by a unit of weight of a fish and the longitudinal position of the fish in the stream.

ACKNOWLEDGMENT

The author is greatly indebted to Professor V. E. Shelford, of the Zoology Department, University of Illinois, under whose direction these experiments were carried out; and to Dr. D. H. Thompson, of the Illinois Natural History Survey, who has been a constant help both during the period of experimentation and in the preparation of this paper.

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FACTORS INFLUENCING THE RATE OF GROWTH OF PINE IN ARKANSAS¹

LEWIS M. TURNER

College of Agriculture, University of Arkansas

The purpose of this study is to determine the possibilities of correlating features of site with height growth rate of *Pinus echinata* and *P. taeda*. Particular emphasis is placed on soil and topographic features, not disregarding, however, the possible effects of differences in the climatic complex.

Previous studies of somewhat similar nature are of two general types: those seeking to correlate certain site complexes, in which soil plays a major role with specific vegetation or forest types; and studies attempting to relate the success or rate of growth of one or more species to various sites. As the title and the foregoing suggest this study more closely resembles the latter type.

As regards the correlation of vegetation, or forest type, with certain site features the following studies are representative. Wherry ('22) concludes that the occurrence of red cedar in the eastern states bears a distinct relationship to available limestone in the soil. Veatch ('28) has suggested the practicability of reconstructing forest cover on the basis of soil maps in Michigan. Tamm ('29) states, "The theory of vegetational types proposed by Cajander and later developed by Malmström is given additional support when soil profiles are studied in connection with vegetation. Where not altered by fire or man forest types in northern Sweden exhibit a remarkable permanence and are determined by soil types." Cain ('31) on the basis of study in the Big Smoky mountains of North Carolina and Tennessee concludes that adjacent plant associations in that region cannot be separated on the basis of reaction (pH) alone, which is in agreement with Coile ('33) who found that soil reaction does not differ greatly enough to be a limiting factor in the distribution of forest types in the Duke Forest in North Carolina. Pearson ('31) working on the relationship of climate and soil to forest types in the southwestern United States, concludes: "Soil rarely acts as a limiting factor in this region except in a local way and in conjunction with climatic limitations. The most important effect of variations in soil is to increase or decrease the amount of moisture available for plant growth." Lunt ('32) in his study of profile characteristics of New England soils, found a limited degree of correlation between occurrence of tree species and type of soil profile. Alway and McMiller ('33) reporting on investigations on a small sandy island in

¹ Research Paper No. 421. Journal Series, University of Arkansas.

northern Minnesota, found that soil differences could not account for differences in forest composition in that area. The slight differences occurring seem to be the result and not the cause of differences in forest type. Wilde ('33) in a study of the relation of soils to forest vegetation in the Lake States Region found general vegetation types and general forest types associated with specific soil situations. Young ('34) on the basis of study of the physical, chemical and electrometric measurements of the Cranberry Lake soil in the west central Adirondack mountains, concludes that a high degree of soil heterogeneity prevails from habitat to habitat in the same relation that vegetation varies in composition.

The following studies are related to the problem of correlation of rate of growth of species with specific site factors: Barth ('28), in a study of the relationship of quality of oak sites and soil particles, found no definite relationship between site quality and size of soil particles. He found that the best sites were those possessing soil with the greatest air capacity, except near the surface, where soil had been modified by cultivation. There was little or no correlation between yields and water absorption, hardness of soil, or humus content. Yield varied with quantity of nitrogen in the first 10 dm. of soil, except for the poorest site where the raw humus contained much nitrogen. Variations in the amount of other elements and acidity had no appreciable effect on site quality. Haig ('29) found that the rate of growth of red pine on brown, weekly podsolized soils in southern Connecticut is related to the colloidal and silt-plus-clay content of the soil. Variations in organic matter and pH are negligible in effect. Knowledge of the texture quality of the **A** horizon, or surface soil, permits classification of soil quality as regards tree growth and in general a means of determining site quality of forest soils. Auten ('30), reporting on the relation of soils of the Mont Alto State Forest in south central Pennsylvania, concludes that volume growth of wood seems to be somewhat independent of soil texture in that area. Factors influencing soil moisture he considered of great importance. Hicock, *et al.* ('31), working with young stands of red pine in Connecticut, found that soil series, soil texture, character of the **A**₁ horizon and character of the sub-soil, each considered individually, could all be correlated with site index, but the degree of correlation is rather low in each case. In general, they did not consider the correlation of the various site factors with site index, as expressed by height increment, entirely successful. Westveld ('33) found little range in rate of height growth between several areas on the same soil type in northern Michigan. Variation in the degree of stoniness of the soil seemed especially influential, in cases where a wide range in rate of height growth did occur on a given soil type. He found that the rate of height growth could be related to certain major characteristics of the soil profile, and thereby, soils could be grouped into five major and two minor groups on the basis of site value.

LOCATION OF STUDY

Three areas, Ashley county in the southeastern corner of the state, Columbia county in the south central, and Howard county in the southwestern part, are those incorporated in the study.

CLIMATE

The climate of the section (U. S. Dept. Agri. '22) is characterized by its short, moderately cold winters, long, warm summers, ample cloudless days, moderate extremes of temperature, high relative humidity and heavy rainfall. There is essential similarity in the climate of all three counties. The mean annual temperature for all of the three areas is near 64° F., highest temperature around 109°, and the lowest near —2° in Ashley county, —4° in Columbia, and —10° in Howard county. A weather observation station in Ashley county reports 54 inches mean annual precipitation and 223 frostless days. The station nearest Columbia county reports 44 inches mean annual precipitation and 235 frostless days, and a Howard county station, 50 inches mean annual precipitation and 221 frostless days. For the most part the rainfall is evenly distributed throughout the year, the average precipitation for the winter months being little less than for the summer months. Severe droughts are not uncommon.

TOPOGRAPHY AND GENERAL CHARACTER OF THE SOILS

Ashley and Columbia counties lie within the coastal plain region, that is, the triangularly shaped southeastern half of the state that was occupied by sea during Cretaceous times (Veatch, '06). The region, outside of the floodplain of the Mississippi river, is characterized by rolling to very flat topography. The elevation of Ashley county ranges from about 160 to 190 feet above sea level, and Columbia county around 300 feet. The soils of Ashley county are predominately upland soils derived from loessial or coastal plain materials; occurring to lesser extent are recent alluvial soils of first stream bottoms, and terrace or second bottom soils. Outside of stream floodplains, flat, poorly-drained silty loams are extensive and sandy loams second in importance. The soils of Columbia county are also mainly of sedimentary origin, but are derived from areas of soil material of the southern Ozark (Ouachita) uplift farther north. The older soils, those other than floodplain soils, are made up of unconsolidated sands, mainly of fine texture, of clays, and to a small extent of ligniferous material. The most common and extensive soils of the uplands are very fine sandy to sandy loams with clay subsoil.

An east-to-west line running a little south of the center of Howard county is the dividing line between the Ouachita mountain region and the coastal plain. Hence the foregoing discussion of Columbia county applies essentially to the southern part of Howard, except the average elevation of the latter is

400 feet. The northern part of the county is dissected by ridges extending east and west for the most part, the elevation is about 800 feet, and the highest point, in the northeastern corner of the county, is 1600 feet. These ridges are the southern margin of the Ouachita uplift and the rocks essentially fine grained sandstone or shale. The soils derived from the sandstones are light colored to reddish brown stony or sandy loams with friable clay subsoil, and the soils from the shales are similar except in color, being red, yellow, or greenish. Extremely stony areas, and exposed rock are of common occurrence on the steeper slopes.

METHOD OF PROCEDURE

The study, made during the spring and summer of 1934, involves the analysis of 125 plots of one-quarter acre each. Only pure pine stands were selected for study and of necessity most of these are "old-field" stands. Obviously little could be learned of the clearing and cropping history of such plots; doubtless a wide range of difference in cultural care has occurred within the entire number of plots studied, or within the number of plots on any soil type. However, the comparatively unimportant effect of this unmeasured variable is revealed by following data. A few plots were in virgin forest, and a larger number in "hurricane forest," a type of essentially pure pine stand which is presumably established in the paths of tornadoes (Turner, '35). Plots were rejected which were obviously understocked as a result of cutting or other factors. No stands were acceptable which were altered to appreciable extent by fire, disease, wind or other destructive agencies. Since very young stands presumably do not afford satisfactory evidence of the actual lumber producing capacity of the site, an arbitrary average age minimum of 50 years was observed in plot selection. Summarily speaking, as far as possible, selection was made of stands which presumably demonstrated the approximate pine-growing capacity of the site types on which they were growing.

On each plot, determination was made of the height, diameter (at breast height), age, and dominance character of all trees. Dominance character refers to whether a tree is dominant, co-dominant, or suppressed. Approximately 2300 trees were so studied. Direction and percentage of slope was recorded. By referring to county soil maps (U. S. Dept. Agri. Bureau of Soils) and to the description of the soils (Nelson, Sachs, Austin, '23) the series-type of the soil in question was determined. This point was established by digging two trenches and by making borings on each plot. Through the agency of these trenches and borings, profile diagrams were made and samples collected at three or four levels to a depth of three and a half feet. Later, pH determinations, and physical analysis by the Bouyoucos method were made of the samples (Bouyoucos, '34).

Comparison of value of sites was made by the determination of the "site index" for each plot, a method familiar to foresters, lumbermen and others

(U. S. Dept. Agri. '29). Site index is the average height of dominant and co-dominant trees at 50 years of age, and is secured by plotting height over age of a suitable number of trees. In several instances the number of trees per plot, or the lack of suitable age spread, did not permit the construction of strong curves. However, by uniting the records of several plots on the same soil and slope, an operation which has proved to be sound and permissible, the weight of numbers and spread of age required to make suitable curves was secured. Employing site index alone for comparing value of sites, means of, course, that height growth alone is used as the criterion of site value. Doubtless a measuring rod integrating volume of timber and age would be a more comprehensive means of evaluating and comparing sites, but since no such scheme is in general use the site index method was employed.

RESULTS

A. The Relationship of Soils Series Type to Rate of Height Growth

In general, there was found a rather high degree of correlation between the rate of height growth and conditions associated with soils of specific series type alone. As would be expected this is more apt to be found in the instances of soils having relatively constant topographic features. Two groups of soils may be set up, (1) those with little variation in topography and in apparent site quality, and (2) those with considerable range in these features. Further, within each of these is recognizable a gradient in the quality of soil types within the group which readily forms the basis for at least a sub-grouping into superior, medium and inferior sites.

1. Soils with Uniform Topography

Ocklockonee fine sandy loam¹ (13), having an apparent site index of 92² for *Pinus echinata* and 108 for *Pinus taeda*, is a soil of the floodplain of small streams in the coastal plain. It is a flat but fairly well drained, alluvial soil, generally immature and loose in texture, and having, because of its topographic position an adequate and constant water supply. The ratio of sand-silt-colloid of the **A**₂ and **B** horizons is high-medium-medium. Vicksburg silt loam (18), having an apparent site index of 107 for *Pinus taeda*, is also an alluvial soil of small stream bottoms, made up of material washed from Caddo silt loam. It is commonly not as well drained as Ocklockonee sandy loam, in considerable measure due to its much lower sand and high silt content, the ratio of sand-silt-colloid in the **A**₂ and **B** horizons being medium-high-high. It is uniform in structure with poorly defined horizons. Presumably on account of these features it is less suited to the requirements of *Pinus echinata*.

¹ See table I for soil analysis data. Figures in parentheses refer to number of soil in tables I and II.

² See table II for site indices of soils.

TABLE I. *Depth of horizons, and physical and electrometric analysis of forest soils of southern Arkansas*

Soil	Horizon	Depth of horizon inches	Sand	Silt	Colloid	pH	County ¹
1. Boeuf fine sandy loam, slope 0-1%	A ₁ A ₂ B	0-11 11-26 26	70 57 44	12 14 20	18 29 36	5.2 4.8 4.6	A
2. Caddo silt loam, slope 0-2%	A ₁ A ₂ B	0-3 3-38 38	36 24 24	46 40 39	18 36 37	5.8 5.0 5.0	A
3. Caddo, very fine sandy loam, slope 3%	A ₁ A ₂ B	0-7 7-20 20	46 41 45	34 27 18	20 32 37	6.0 4.8 4.6	C H
4. Caddo-Ruston transition, slope 0-2%	A ₁ A ₂ B	0-7 7-22 22	53 49 43	24 20 25	23 31 32	6.0 5.4 5.2	A
5. Greenville gravelly loam, slope 10%	A ₁ A ₂ B	0-8 8-21 21	42 34 30	28 16 13	30 50 57	5.3 4.8 4.8	H
6. Hanceville fine sandy loam, slope 5% (plateau)	A ₁ A ₂ B	0-6 6-19 19-33	75 69 46	11 11 6	14 20 48	5.3 5.3 5.0	H
7. Hanceville fine sandy loam, slope 5% (gully)	A ₁ A ₂ B	0-3 3-14 14-34	71 65 59	15 16 14	14 19 27	5.5 5.1 4.6	H
8. Hanceville fine sandy loam, slope 7%	A ₁ A ₂ B	0-4 4-16 16-37	60 61 59	12 18 11	28 21 30	5.1 5.1 4.7	H
9. Hanceville fine sandy loam, slope 13%	A ₁ A ₂ B	0-3 3-17 17	63 60 42	16 15 13	21 25 45	5.1 4.9 4.5	H
10. Hanceville find sandy loam, slope 25%	A ₁ A ₂ B	0-3 3-12 12-30	57 48 46	18 15 14	25 37 40	6.0 5.0 4.8	H
11. Lufkin silt loam, slope 0-1%	A ₁ A ₂ B	0-7 7-22 22	27 26 23	51 46 34	22 28 43	5.4 4.7 4.7	C
12. Norfolk fine sandy loam, slope 2.5%	A ₁ A ₂ B	0-8 8-27 27-35	70 59 60	17 12 16	13 29 24	5.8 5.3 5.0	C H
13. Ocklockonee sandy loam, slope 0-1%	A ₁ A ₂ B	0-10 10-29 29	55 53 47	26 24 28	19 23 25	5.2 4.8 4.8	C H

TABLE I. (Continued)

Soil	Horizon	Depth of horizon	Sand	Silt	Colloid	pH	County ¹
		<i>inches</i>					
14. Ruston fine sandy loam, slope 2.5%	A ₁	0-6	53	27	20	6.4	A C H
	A ₂	6-21	44	30	26	5.4	
	B	21	49	19	32	5.0	
15. Ruston fine sandy loam, slope 6%	A ₁	0-9	48	33	19	6.0	A C H
	A ₂	9-25	48	38	24	5.0	
	B	25	43	22	35	4.6	
16. Susquehanna fine sandy loam, slope 4%	A ₁	0-9	58	19	23	5.4	C H
	A ₂	9-27	45	17	38	4.5	
	B	27	45	16	39	4.5	
17. Susquehanna fine sandy loam, slope 9%	A ₁	0-10	66	15	19	5.4	C H
	A ₂	10-37	55	13	32	5.0	
	B	37	47	9	44	4.6	
18. Vicksburg silt loam, slope 0-1%	A ₁	0-5	25	38	37	6.0	A
	A ₂	5-15	28	37	35	5.0	
	B	15	29	32	39	5.0	

¹ Indicating the counties in which the soil occurs: A, Ashley; C, Columbia; and H, Howard.

TABLE II. *Site indices of Pinus echinata and Pinus taeda on soils of southern Arkansas*

Soil	Per cent slope	No. of plots	<i>Pinus echinata</i>			<i>Pinus taeda</i>		
			No. of trees	Site index	A.R.S.I. ¹	No. of trees	Site index	A.R.S.I. ¹
1. Boeuf fine sandy loam	1	4				66	94	91-96
2. Caddo silt loam	2	22	175	90	84-101	232	92	84-100
3. Caddo very fine sandy loam	3	8	81	78	74-80	73	83	77-85
4. Caddo-Ruston transition	2	3	26	89	88-94	35	89	85-90
5. Greenville gravelly loam	10	5	65	70	64-72			
6. Hanceville fine sandy loam (plateau)	5	3	50	80	none			
7. Hanceville fine sandy loam (gully)	5	3	30	65	65-70	14	77	74-75
8. Hanceville fine sandy loam	7	4	63	65	60-75			
9. Hanceville fine sandy loam	13	5	87	53				
10. Hanceville fine sandy loam	25	4	76	45				
11. Lufkin silt loam	1	5				54	85	83-95
12. Norfolk fine sandy loam	2.5	6	67	68	66-75	55	69	65-75
13. Ocklockonee sandy loam	1	5	15	92	none	60	108	102-110
14. Ruston fine sandy loam	2.5	10	89	83	80-92	89	84	83-90
15. Ruston fine sandy loam	6	3	32	72	60-79	25	74	none
16. Susquehanna fine sandy loam	4	11	120	75	70-82	103	77	71-81
17. Susquehanna fine sandy loam	9	7	85	73	72-76	76	76	75-77
18. Vicksburg silt loam	1	4				75	107	100-108

¹ Apparent range in site index.

Boeuf fine sandy loam (1), has an apparent site index of 94 for *Pinus taeda*. It is somewhat similar to Ocklockonee sandy loam, but is commonly sandier, and with more slope, often making up low ridges in the bottoms of larger streams. *Although exhibiting rather wide variation in the depth of its horizons, its site index for *Pinus taeda* varied little from the figure given above. The ratio of sand-silt-colloid of its A_2 and B horizons is high-low-medium. Its water supply is doubtless satisfactory but probably inferior to the foregoing types. Caddo silt loam (2) with a site index of 90 for *Pinus echinata* and 92 for *Pinus taeda* is a soil of wide extent in southeastern Arkansas. It is a flat soil with a very silty A_1 horizon, the ratio of sand-silt-colloid in the A_2 and B horizons being medium-high-high. Its water supply is presumably always adequate on account of its flatness and resultant imperfect drainage. Rather extensive, very flat, phases of Caddo silt loam in this region are still occupied by a prairie association (Wackerman, '29). A transition type of soil, lying between areas of Caddo silt loam and Ruston fine sandy loam (4) is also a superior pine growing soil, having an apparent site index of 89 for both *Pinus echinata* and *P. taeda*. It has a rather high sand content of the A_1 horizon and the ratio of sand-silt-colloid in the A_2 and B horizons is high-medium-medium.

Within the two following sub-groups occur some soils that doubtless have some variation in slope, namely Caddo very fine sandy loam (3), Greenville gravelly loam (5) and Norfolk fine sandy loam (12). During the course of the study, however, only areas of the approximate slope indicated were encountered, hence their inclusion in this main group.

Some soils of the first group, of medium site value, are as follows: Lufkin silt loam (11) with a site index of 85 for *P. taeda*, is similar to Caddo silt loam as regards its origin, structure and topography. Differences which possibly account for its lower site value are the somewhat higher colloid and silt content of its B horizon and the fact that this layer is within 22 inches of the surface in Lufkin and 38 inches from the surface in Caddo silt loam. Probably this more impervious layer nearer the surface, resulting in a wetter, more poorly ventilated soil, accounts for the sparing occurrence of *P. echinata* on this soil. Caddo very fine sandy loam (3) is a rolling soil with a relatively high sand content in all horizons, and relatively high colloid content of its A_2 and B horizons. The site index of this soil is 78 for *P. echinata* and 83 for *P. taeda*.

Soils in the first group with relatively low site value are as follows: Greenville gravelly loam (5) is a rolling, well drained soil occurring near the southern edge of the Ouachita foothills. Having a site index of 70 for *P. echinata*, it does not seem to be suited to the requirements of *P. taeda*, except in occasional gullies. As its name implies, it usually has much gravel in all horizons. Also possibly contributing to its lower site value, is the low silt and high colloid content of its A_2 and B horizons, the former within 8 inches of the surface. Norfolk fine sandy loam (12) is a rolling, well-drained soil

of the upper coastal plain region. It has an apparent site index of 68 for *P. echinata* and 69 for *P. taeda*. Its low site value may possibly be attributed to the very high sand, low silt and medium to low colloid content of all of its horizons.

2. Soils with Considerable Observed Variation in Topography

The less-sloping phases of Ruston fine sandy loam (14) (slope around 2.5 per cent) have apparent medium site value for pine, that is, 83 for *P. echinata* and 84 for *P. taeda*. This is a soil having a rather high sand and medium silt and colloid content of all horizons. Phases of Ruston fine sandy loam (15) with slope around 6 per cent are inferior to the foregoing, having a site index of 72 for *P. echinata* and 74 for *P. taeda*. As regards the plots studied, the essential difference between these two phases, in addition to degree of slope, is the slightly lower sand and slightly higher silt content of all horizons of the steeper phase.

Susquehanna fine sandy loam, common throughout the coastal plain, shows to lesser extent the same growth response as Ruston fine sandy loam in respect to the effect of degree of slope. Phases of Susquehanna (16) with slope around 4 per cent have an apparent site index of 75 for *P. echinata* and 77 for *P. taeda*. In the plots studied this soil was characterized by a relatively high sand and low silt content in all horizons, and relatively high colloid content of the **A**₂ and **B** horizons, the former with 38 per cent, within 9 inches and the latter within 27 inches of the surface. Phases of Susquehanna fine sandy loam (17) with slope around 9 per cent were only slightly lower than with the less-sloping phase, being 73 for *P. echinata* and 76 for *P. taeda*. This more sloping phase also differed in its somewhat higher sand and lower silt content of all horizons.

Hanceville fine sandy loam with its numerous variations as regards degree of slope and stoniness is one of the most extensive soils in the Ouachita mountain region. A relatively flat, or plateau phase (6) of this soil, differing from other phases in being free from stone, has an apparent site index of 80 for *P. echinata*, *P. taeda* apparently not occurring on this phase in this region. Resembling other phases of this soil all horizons have a relatively high sand and low silt content in all horizons, colloid content medium in the **A** horizon and relatively high in the **B** horizon which is 19 inches from the surface. A gulley bottom phase (7) made up, of course, of material washed from Hanceville fine sandy loam including stone, with slope around 5 per cent, has a site index of 65 for *P. echinata* and 77 for *P. taeda*. On such sites are found some very large, but very old pines. This phase differs from others in its somewhat lower colloid and higher sand content. Hillside phases with slope around 7 per cent (8) have an apparent site index of 65 for *P. echinata*, with *P. taeda* absent. It is characterized by much stone and relatively high sand, low silt, and medium colloid material in all horizons. Steeper phases with

slope around 13 per cent (9) have an apparent site index of 53 for *P. echinata*. This phase has much stone and a relatively high sand and low silt content, and high colloid content of the **B** horizon, which is within 17 inches of the surface. Steeper phases with slope around 25 per cent (10) have an apparent site index of 45 for *P. echinata*, with *P. taeda* again absent. This phase has much stone and a slightly lower sand content than the foregoing, and an **A**₂ horizon containing a relatively large amount of colloid (37 per cent) within 3 inches of the surface, and a **B** horizon containing 40 per cent within 12 inches of the surface.

B. The Relationship of Variation in Other Factors to Rate of Height Growth

Within the limits of the number of plots that could be studied of any given slope of any given soil a fair representation of variation in exposure was secured. However, no variation in site quality could be correlated with this factor alone. As regards soil reaction, because of more complete data, a similar but more conclusive statement may be made. In the available publications on the mineral nutrient content of the soils of the region the following information is supplied: Hanceville fine sandy loam is described as having medium to low nitrogen and phosphorus, Norfolk fine sandy loam with low nitrogen and phosphorus, Susquehanna fine sandy loam with low nitrogen and phosphorus, Caddo silt loam with medium nitrogen and low phosphorus, and Vicksburg silt loam presumably with medium nitrogen and low phosphorus. In other words, it seems that of the soils studied, some affording both superior and inferior site indices have low phosphorus and low or medium nitrogen; none are superior as regards this factor. Attention should be called to the fact, however, that the four superior soils studied, Ocklockonee, Vicksburg, Boeuf, and Caddo silt loam, and one of intermediate value, Lufkin silt loam, are more apt to be in virgin condition than any of the others except the sloping phases of Hanceville. The former were not as often cleared of timber and farmed because of their poorly drained nature, or of the fact that they are in floodplains; the latter because of its steepness or stoniness. It seems probable that mineral analysis of the soils of the actual plots might reveal a relationship between this factor and rate of growth, not only as regards the difference in quality between soil types, but the difference in quality of plots on the same soil and slope. Such analyses are not available.

DISCUSSION

According to this study the following soil types or phases of soil types can be classified as superior as regards the grade of height growth of pine associated with them: for *Pinus taeda*—Ocklockonee sandy loam, Vicksburg silt loam and Boeuf fine sandy loam. For *Pinus echinata* and *P. taeda*—Caddo silt loam and Caddo silt loam-Ruston fine sandy loam transition. Soils af-

for medium site quality for *Pinus taeda*—Lufkin silt loam; for *Pinus echinata*—Hanceville sandy loam of 5 per cent slope (plateau phase); for both species—Ruston fine sandy loam, Caddo very fine sandy loam and Susequahanna fine sandy loam. Soils affording inferior site quality for *Pinus echinata* are: Greenville gravelly loam, Norfolk fine sandy loam and Hanceville sandy loam with slope ranging from 7 to 25 per cent.

Quality or quantity of site factors associated with superior sites seem to be as follows: (a) Flat, or slightly sloping soils with resulting adequate water supply but with more or less permeable subsoil; (b) soils may vary considerably in the nature and structure of their horizons, the A_2 and B horizons being high-medium-medium, medium-high-high, or high-low-medium as regards the proportion of sand-silt-colloid; (c) soils with the B horizon silty clay or clayey silt not closer than 15 inches to the surface, or clayey sand and silty sand two feet or more from the surface; (d) recent alluvial soils, immature and not strongly stratified; (e) soils as described above in the virgin state or on which the forest had been removed near the middle of the last century, farmed for a short time, and allowed to go back to timber; and (f) soils which are reported as having medium nitrogen and low or medium phosphorus content.

Sites of intermediate quality seem to be associated with the following: (a) Flat, silty soils with the B horizon containing 43 per cent colloidal material, 34 per cent silt, and 23 per cent sand within 22 inches of the surface, apparently rather poorly drained and aerated, with medium nitrogen and low phosphorus, commonly in the virgin state; (b) rolling, sandy loams, with friable or plastic clay B horizon within 20 inches or less of the surface, horizon may have high-medium-medium, high-low-high, high-medium-high, or medium-high-high sand-silt-colloid content of the A_2 and B horizons; and (c) Soils as described above that were farmed more or less fifty years ago.

Sites of inferior quality seem to be associated with the following: (a) Rolling, or hilly, extremely gravelly soils with sandy or gravelly A_2 horizon containing 50 per cent colloidal material, within 8 inches of the surface; (b) soils with rolling to hilly topography and very high sand content in all horizons; and (c) very stony, sandy loams with slope varying from 7 to 25 per cent, with high-low-medium, or high-low-high sand-silt-colloid content in the A_2 and B horizons, the B horizon containing 40 to 45 per cent colloid within 12–17 inches of the surface.

It seems apparent from the foregoing that degree of slope, and its effect on drainage, and the depth, or spatial relationship, and physical structure of the A_1 , A_2 and B horizons, as affecting available water, are important factors influencing the rate of growth of the trees in question. This conclusion bears a certain relationship to Haig's and Westveld's conclusions, and is in essential agreement with that of Auten bearing on this general factor. The author agrees with Hicock, *et al.*, that rate of growth cannot be correlated with any single factor, but rather is dependent on the interaction of several factors.

The present study confirms the opinion of Barth and Haig that variation in soil reaction is negligible in effect as regards the rate of growth of these pines, on the sites studied. The findings of this study partially agree with those of Westveld's that there occurs little range in the rate of height growth on several areas on the same soil, except in instances where there occurred considerable variation in the topography of a given soil. This study also agrees with Westveld's that soils can be satisfactorily grouped according to site value.

A recognized difference (Mattoon, '26, '27) in the site preferences of these two presumably closely related pine species is reaffirmed by this study. In the region studied *Pinus taeda* is usually associated with soils that are comparatively flat, often with poor drainage. Site indices ranged from 74 to 108 in such situations. Apparently this species occurs irregularly on soils with more than 5 per cent slope. *Pinus echinata* was absent on two and present on one soil superior for *P. taeda*. In this latter instance the site index of *P. echinata* was much lower than that for *P. taeda*, whereas on most soils supporting both species, the site indices were similar. As suggested, *P. echinata* is distinctly better adapted to steeply sloping soils than *P. taeda*. Within the range of site conditions studied site indices of *P. echinata* varied from 45 to 92.

It is recognized, of course, that the site values obtained for these site complexes have significance only within regions having comparable climate. Within this limitation, however, it seems possible that such a method of study covering a more complete range of site conditions would yield information of considerable silvicultural value. Such data could be used as a basis for the prediction or close approximation of the potentialities of specific sites as regards the rate of growth of the species in question. This might well be an important element in the foundation of a planned, statewide or regional forestry program.

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CONCLUSIONS

1. One-hundred and twenty-five one-quarter acre plots of *Pinus echinata* and *Pinus taeda* on 18 soil types or phases of these types were studied in an attempt to correlate rate of growth of these species with quality of site factors.
2. Comparison of quality of sites was made on the basis of the rate of height growth afforded by the site.
3. A rather high degree of correlation was found between the rate of height growth and soil series type alone, particularly as regards soils with little variation in topography.
4. A higher degree of correlation was found between the rate of height growth and degree of slope of soil series types.

5. Sites affording the highest site indices are those on soils that are immature, flat, of high silt or silty sand content, with permeable subsoil and hence at least fair drainage but with obvious adequate water supply. Generally these soils have been farmed little or none. Sites with intermediate value are those on soils that are either flat with apparent more or less impermeable subsoil relatively near the surface, or rolling, sandy loams with friable or plastic clay subsoil relatively near the surface (10–20 inches). Such soils usually have been farmed considerably. Sites with lower site indices are on soils with a high degree of slope and hence excessive water run-off, or extremely stoney, gravelly, or sandy soils with moderate or steep slope, commonly with rather stiff but friable sandy clay subsoil within 12–16 inches of the surface. Such soils have been farmed little or none.

Site indices could be correlated with quantitative group combinations of factors such as are summarized in a specific soil with specific slope, but not with any one factor or grade of factor.

6. The results obtained indicate the practicability of the method in predicting the tree growing potentialities of recognizable site complexes.

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THE EFFECT OF HUMIDITY ON THE DEVELOPMENT OF THE WEBBING CLOTHES MOTH (*TINEOLA BISSELLIELLA* HUM.)

GRACE H. GRISWOLD AND MARY F. CROWELL

Cornell University

The webbing clothes moth (*Tineola bisselliella* Hum.) may be found in well-heated houses at all seasons of the year, although the adults occur in greatest numbers in spring and summer. Only occasionally are the moths seen flying about a house during the winter months. Because of the present interest in air conditioning it is important to determine the effect of humidity on this common pest. Some observations on the subject have already been made. Haines ('32) says that, "dampness appears to favour the spread of every species of clothes moth," but he does not give the data on which he bases this statement. Mellanby ('34) subjected larvae of the common clothes moth (*Tineola bisselliella* Hum.) to varying conditions of temperature and humidity in order to study the effect on their metabolism. In a summary he says, "the results suggest that the rate at which water is evaporated from the larvae is proportional to the saturation deficiency of the air." Titschack ('25, '27), in his studies on the effect of temperature on *T. bisselliella* conducted some experiments at low and at high humidities, using calcium chloride for the dry atmospheres, and wet sand for the humid ones. At a temperature of 30° C. he found that development was more rapid in the moist situation.

According to Flora ('17) ". . . in the winter season a majority of persons in the northern part of the United States live in an indoor climate that is ultra-desert in regard to moisture conditions." During the months of November and December, 1909, at Topeka, Kansas, Flora made daily observations on the relative humidity in a steam-heated office. His observations were made at 8:00 A.M., at noon, and at 4:00 P.M. For all of the relative humidities determined the maximum was 56 per cent and the minimum 14 per cent, while the mean of all observations was 28.4 per cent. Ward ('02) in Massachusetts, made similar observations during three weeks in November, 1899. His records show a maximum of 40 per cent, a minimum of 24 per cent, and a mean of 30 per cent, thus differing but slightly from Flora's observations. The United States Weather Bureau at Ithaca has kindly furnished us with data covering several years, on the out-door relative humidities determined at Ithaca during the months of June, July, and August. The observations were made daily at 8:00 A.M., at noon, and at 8:00 P.M. The means for the three daily observations were as follows: June 70 per cent, July 68 per cent, and

August 71 per cent. It is probable that, during the summer months, the relative humidity indoors does not vary greatly from that outdoors. These data indicate that the relative humidity in furnace-heated houses in winter is less than half what it is in summer. Can this high humidity of the spring and summer months be correlated with the presence of greater numbers of clothes moths at these seasons?

The data to be presented in this paper were obtained from two series of experiments. The first experiments were carried on during the winter of 1933 and '34, and the second series during the winter of 1934 and '35.

EXPERIMENTAL STUDIES

All of the experiments to be discussed were conducted in an incubator at a constant temperature of $25^{\circ}\text{C.} \pm 1^{\circ}\text{C.}$ For the first series three relative humidities were selected—43 per cent, 75 per cent, and 93 per cent. These humidities were maintained in tightly-sealed glass desiccators and museum jars with saturated solutions of the following salts: K_2CO_3 , NaCl , and KNO_3 (Spencer, '26). An excess of salt was always present in contact with the solution. For the second series of experiments it was decided to use two lower relative humidities, 20 per cent and 32 per cent, which were maintained with saturated solutions of $\text{KC}_2\text{H}_3\text{O}_2$ and MgCl_2 (Spencer, '26). In addition, experiments were again conducted at 75 per cent (maintained with NaCl) since, of the three relative humidities used the year before, 75 per cent was found to be the one most favorable for the insects. The equipment in the second series of experiments was standardized to museum jars only (see fig. 1). The flange of the jar and the rim of the cover were ground to make a tight seal possible.

The procedure in both series of experiments was practically the same. Glass shell vials, 2 cm. in diameter and from 3 to 4 cm. in height, were used as containers for the insects. Each of the vials had previously been numbered with a diamond marking pencil, thoroughly cleaned and weighed. In each vial was placed about one gram of fish meal which had been ground through the half-millimeter screen of a Wiley mill. Thus moisture determinations could be made by simply removing the vial with its contents, weighing, drying to constant weight and then reweighing.

Preliminary moisture determinations were made to find the length of time necessary to bring the fish meal into equilibrium with each of the humidities mentioned above. It was found that at the end of eight days the fish meal had attained a constant moisture value in all cases except that of the KNO_3 solution where it never reached equilibrium. Table I gives the final moisture content of the fish meal at the various relative humidities.

For the experiments the vials were prepared and weighed as before and exposed to the atmospheres of the various humidities for ten days, in order that the fish meal might reach equilibrium. To secure eggs, adult moths were

TABLE I. *Moisture content of fish meal at equilibrium with various relative humidities*

Relative humidity	Moisture content
20%.....	5.80%
32%.....	6.84%
43%.....	8.55%
75%.....	12.21%
93%.....	equilibrium not reached

placed in glass jars with clean pieces of black broadcloth. The pieces of cloth were removed late in the afternoon of the same day, thus all eggs were laid on a definite day between 8:30 A.M. and 5:30 P.M. The eggs were kept in the incubator at 25° C. but no effort was made to control the humidity during the egg stage.

As soon as the eggs hatched¹ the larvae were placed singly in the vials described above. Each vial was covered with a piece of fine muslin and the vials were then set in wire baskets suspended above the different salt solutions (fig. 1). In the first series of experiments one desiccator and one mu-

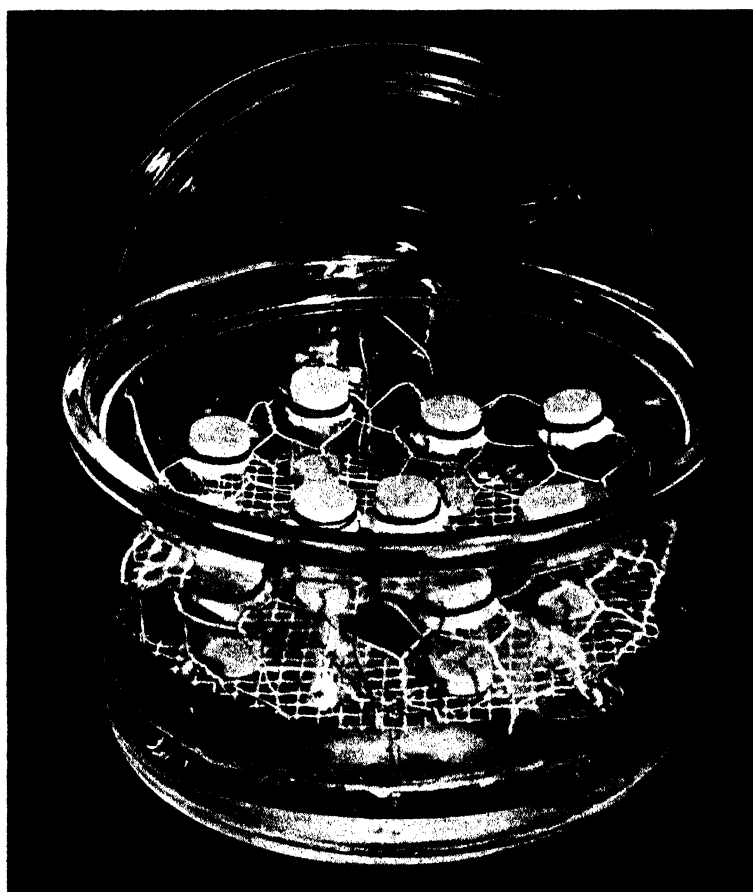


FIG. 1. Museum jar used for maintaining constant humidity with a few shell vials in place above the salt solution.

¹ The egg stage averaged 6.06 days.

seum jar were used for each of the three salt solutions. For each humidity 30 vials were marked for life-cycle and adult-life studies while 20 vials were marked for moisture determinations. In the second set of experiments museum jars only were used as already explained, and 30 vials were marked for life-cycle and adult-life studies while 30 vials were marked for moisture determinations.

The desiccators and museum jars were aerated every other day during the first month. After that they were aerated every day, since it became necessary to make daily examination of the individual vials to determine the date of emergence of adult moths. During the period covered by the experiments two vials were removed each week for moisture determinations. Since it is rather difficult to measure relative humidity by mechanical means in small compartments, this method of weekly sampling served as a check on the maintenance of constant atmospheric conditions. The clothes-moth larva lives surrounded by its food. Therefore, the importance of changes in humidity will depend largely on the effect of these changes on the moisture content of the food.

Figure 2 shows in graphic form the values obtained over a period of nine weeks. It will be noticed that the percentage of moisture for each relative

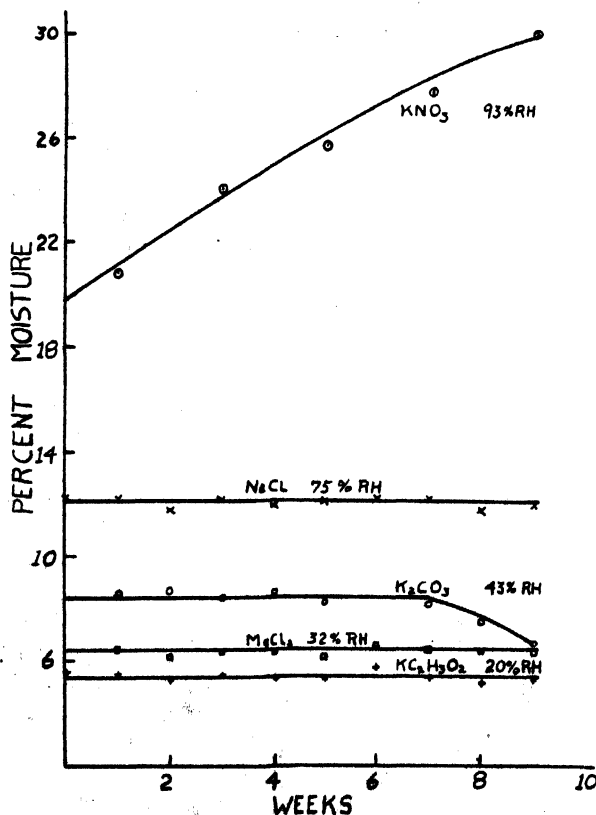


FIG. 2. Moisture content of fish meal containing clothes moths.

humidity remained practically constant throughout the period except in the KNO_3 jars (93 per cent relative humidity). The fish meal exposed to 93 per cent relative humidity never attained equilibrium and developed a mold infestation about five weeks after the larvae were placed in the vials. The drop in moisture content of the fish meal at 43 per cent relative humidity toward the end of the period cannot be explained. A similar drop was not observed in the other relative humidities, 75 per cent, 32 per cent, and 20 per cent.

Fish meal is a food which has been found to be highly satisfactory to the webbing clothes moth (Griswold, '33). Since this material is not kept on hand in the ordinary home and is not generally available to clothes moths, it seemed advisable to determine the percentage of moisture in some materials that are commonly attacked by these insects and compare it with the moisture content of fish meal. Feathers and black woolen broadcloth were chosen for this purpose. The barbs of the feathers were removed from the shaft and then cut into very small pieces, while the broadcloth was snipped into similar tiny bits. The pieces of feathers and of broadcloth were placed in small shell vials and exposed to the atmospheres of the three humidities used in the last set of experiments until equilibrium had been reached. Moisture determinations were then made by the usual method. Table II shows the moisture

TABLE II. *Moisture content of broadcloth, feathers, and fish meal under varying conditions of relative humidity*

Materials	Percentage of moisture		
	20% r.h.	32% r.h.	75% r.h.
Feathers	5.92	7.17	11.87
Broadcloth	5.49	6.50	10.98
Fish meal	5.80	6.84	12.21

content of broadcloth, feathers, and fish meal at the three humidities used in the last series of experiments. It is evident from this table that the moisture values of such materials as broadcloth and feathers, which are often infested by clothes moths, show the same trend as fish meal when exposed to similar atmospheric conditions.

After the last adult had died, the remaining vials, from which no moths had emerged, were kept under daily observation for a period of three months, when it seemed probable that the insects in these vials must have died. In order to determine, if possible, the stage in which death had occurred, the fish meal in each vial was carefully examined under a binocular microscope. The results of this examination will be found in table V. The fish meal in the vials kept at 93 per cent relative humidity was so wet and soggy at the end of the experiment that it was difficult to handle. As noted in the table, fully-formed pupae were found in two of the vials, but the stage in which the other individuals died could not be determined with certainty, since some of the specimens were so badly decayed.

DISCUSSION

The data obtained from the two series of experiments can best be given by organizing the matter in tabular form. Table III shows clearly that development is retarded in dry atmospheres, since the life cycles of both males

TABLE III. Length of life cycle under different percentages of relative humidity

Percentage relative humidity	Sex	Life cycle in days		
		Max.	Min.	Average
20%	Males	78	54	60.78
32%	Males	65	51	54.11
43%	Males	51	46	48.81
75% ²	Males	48	40	42.55
75%	Males	45	39	41.06
93%	Males	55	45	49.00
20%	Females	73	56	61.93
32%	Females	69	52	59.56
43%	Females	62	50	53.82
75% ²	Females	50	46	47.71
75% ³	Females	47	43	45.20
93%	Females	69	45	54.75

² First series of experiments.

³ Second series of experiments.

and females were longer at a relative humidity of 20 per cent than under more moist conditions. The shortest life cycles for both males and females occurred at a relative humidity of 75 per cent. Unpublished data obtained by the senior author show that in *Tineola bisselliclla* the life cycle of the female is consistently longer than is that of the male.

In table IV will be found the number of adults reared at the five humidities used. Here the differences are not so striking since practically as many adults emerged at relative humidities of 43 per cent and 32 per cent as at 75 per cent. A glance at table V, however, shows that, of the five individuals which failed to emerge in an atmosphere of 75 per cent relative humidity, two died as pupae and two as fully grown larvae. Just why these individuals failed to develop into adults it is not possible to say. It should be noted that, even at a relative humidity as high as 93 per cent and in spite of a mold infestation, over half of the larvae completed their development and emerged as adults. And, of the ten that failed to emerge, at least two reached the pupal stage before they died. As already stated, the fish meal in the vials kept at 93 per cent relative humidity was wet and soggy by the end of the experiment. As a result, the dead insects present in these vials were in such a condition that it was not always possible to determine in what stage death occurred.

Table VI gives the length of the adult life under the five humidities. Here again we find that a relative humidity of 75 per cent was most favorable to the insects, since both males and females lived longer than in the other

TABLE IV. *Number of adults reared under different percentages of relative humidity*

Percentage relative humidity	Number larvae	Adults reared		
		Males	Females	Total
20%	30	9	15	24
32%	30	9	18	27
43%	30	16	11	27
75% ⁴	30	11	17	28
75% ⁵	30	17	10	27
93%	30	10	8	18

⁴ First series of experiments.⁵ Second series of experiments.

atmospheres. Griswold ('31) has shown that among adults of *Tincola biselliella* the males live much longer than do the females.

Attention should be called to the fact that in the second series of experiments the results obtained at a relative humidity of 75 per cent checked very closely with the results obtained at this humidity in the first experiments. Where a relative humidity of 75 per cent was maintained conditions were found to be most favorable for the insects as evidenced by the following facts: *a*, the life cycles for both males and females were the shortest (table III);

TABLE V. *Stage in which death occurred among the individuals which did not emerge as adults*⁶

Percentage relative humidity	Stage in which death occurred		
	Larval	Pupal	Total
20%	6	0	6
32%	3	0	3
43%	3	0	3
75% (1st. series)	1	1	2
75% (2nd. series)	2 ⁷	1	3
93%	10 ⁸	2	12

⁶ Unless pupae were present it was assumed that the insects died in the larval stage even if the actual specimens could not be found.⁷ Fully grown larvae.⁸ Some of these may have been pupae (see text).

b, the highest percentage of larvae completed their development and emerged as adults (table IV); *c*, the adults, both males and females, lived the longest (table VI).

The webbing clothes moth has been a household pest for a long period of time and it is, therefore, adapted to a wide range of conditions. Since the only water which this insect consumes is that present in its food, variations in relative humidity may be expected to act by changing the moisture content of the food as well as by influencing evaporation from the surface of the insect. Babcock ('12) showed that larvae of the case-making clothes moth (*Tinea pellionella* Linn.) could complete their development on foods of very low moisture content. He ascribed the successful development in these media

TABLE VI. *Length of adult life under different percentages of relative humidity*

Percentage relative humidity	Sex	Adult life in days		
		Max.	Min.	Average
20%	Males	24	21	22.78
32%	Males	27	14	21.11
43%	Males	34	23	27.25
75% ⁹	Males	37	28	33.45
75% ¹⁰	Males	36	26	31.35
93%	Males	29	5	20.80
20%	Females	22	9	14.40
32%	Females	25	11	15.11
43%	Females	19	12	15.27
75% ⁹	Females	29	12	20.06
75% ¹⁰	Females	23	15	19.00
93%	Females	17	3	8.88

⁹ First series of experiments.¹⁰ Second series of experiments.

to the very important rôle which is played in such cases by water derived from metabolic processes. Analyses of clothes moth excrement revealed that the various constituents were present in such proportions that the insects had derived the highest possible amount of water from the oxidation of nutrients. The end products were highly insoluble so that little water was wasted in their removal. In other words, with a low water intake the case-making clothes moth forms the greatest amount of water possible and wastes the least possible.

Mellanby ('34) has shown that in moderately dry or in moderately moist air fasting larvae of the webbing clothes moth (*Tineola bisselliella*) were able to maintain their water balance but that in very dry air the proportion of solid matter in their bodies rose, and in very moist air it fell.

The effect of various relative humidities on the time required for the completion of the life cycle of *Tineola bisselliella* is shown graphically in figure 3. These results indicate that development at 25° C. may proceed under various degrees of relative humidity but that there is an optimum point somewhere near 75 per cent R. H.

SUMMARY

Experiments were conducted at a constant temperature of 25° C. \pm 1° C. and at relative humidities of 20 per cent, 32 per cent, 43 per cent, 75 per cent, and 93 per cent.

A relative humidity of 75 per cent proved to be the one most favorable for the development of the insects as evidenced by the following facts:

a. The life cycles for both males and females were shorter than those obtained in any of the other humidities.

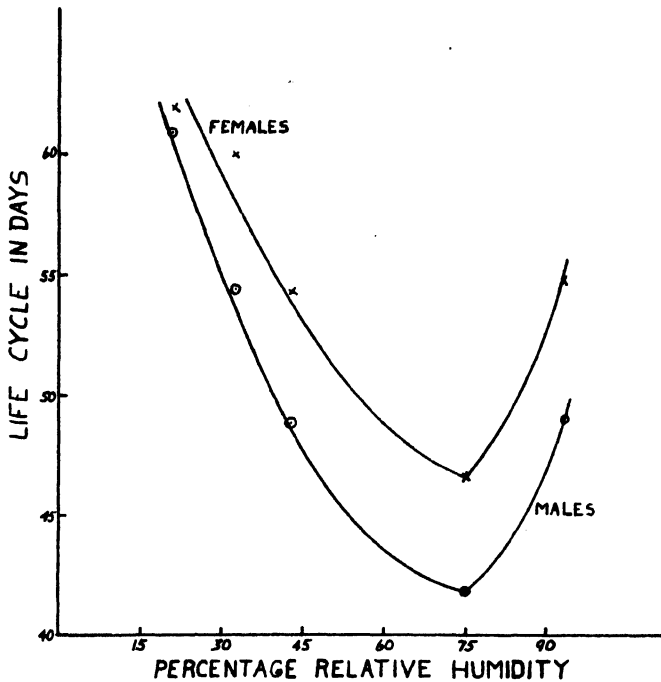


FIG. 3. Effect of humidity on the life cycle of *Tineola bisselliella*.

b. The highest percentage of larvae completed their development and emerged as adults in the 75 per cent relative humidity.

c. The adults, both males and females, lived longer than did those in any other humidity.

The data presented in this paper suggest that the percentage of relative humidity in a dwelling house may have some effect on the number of clothes moths present. The dry atmosphere of the ordinary home in winter would retard development, while the more humid conditions of spring and summer would accelerate it, thus resulting in the presence of fewer moths in winter and of more moths during the spring and summer. However, other factors such as temperature and the quality of the food available must not be overlooked.

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AGE-SIZE RELATIONSHIPS OF HEARTS CONTENT, A VIRGIN FOREST IN NORTHWESTERN PENNSYLVANIA

H. F. MOREY

*Allegheny Forest Experiment Station*¹

The dearth of information concerning the age and size relationships of rapidly disappearing virgin forests stimulated the study of these relationships at Hearts Content, a virgin hemlock-pine-hardwood forest in northwestern Pennsylvania. The present paper discusses the relationship of age, height, and diameter for the principal species in the area.² The location, history, and composition of the stand have been previously discussed (Lutz '30, '34; Morey '35).

METHOD OF STUDY³

Some 200 trees of all species were measured for d.b.h.,⁴ total height, and stump age as they were cut, and d.b.h. and total height were obtained from nearly 600 additional trees in the reserved area. Since the use of increment borers in the reserved area is prohibited, the additional stump ages, approximately 600 in number, were obtained in the cut-over area.

Stump taper measurements for converting diameter at stump height to d.b.h. were taken of approximately 500 standing trees of all species, and bark thickness was obtained from 80 hemlocks, *Tsuga canadensis* (L.) Carr.⁵ for converting the breast high diameter inside bark of peeled trees to diameter outside bark.

Stump ages were converted to total ages by using seedling analyses obtained from over 400 seedlings of all species. These seedlings except those of white pine and white oak, *Quercus alba* L., were obtained in the cut-over area. Because no white pine or white oak seedlings could be found in the

¹ Maintained by the Forest Service, United States Department of Agriculture at Philadelphia, Pennsylvania, in cooperation with the University of Pennsylvania.

² Acknowledgment is due to Assistant Professor Lutz of the Yale School of Forestry for suggestions and criticism of the manuscript, and to the staff of the Allegheny Forest Experiment Station for their aid in the field and office. The writer wishes to thank those also who kindly responded to his inquiry concerning known maximum age and size data.

³ The details of the method of study are filed at the Allegheny Forest Experiment Station.

⁴ Diameter breast high.

⁵ The nomenclature is that of Sudworth's check list. The common names of northern white pine (*Pinus strobus* L.), eastern hemlock and cucumber magnolia (*Magnolia accuminata* L.) are respectively shortened in this paper to "white pine," "hemlock," and "cucumber."

cut-over area, these seedlings were obtained from a culled area adjacent to the hemlock-beech association.⁶ Since it is believed that the present trees at Hearts Content were established in partial shade in more or less localized openings (Morey, '35) rather than in the open, only those seedlings grown in partial shade were selected for analyses. Any seedling which showed release due to cutting was discarded. The average number of years required for the various species to attain given stump height are shown in table I.

TABLE I. *Average number of years required for principal species at Hearts Content to reach various stump heights*

Species	Height—Feet				No. of seedlings	Standard error \pm
	1	2	3	4		
	Age—Years					
Beech	5	8	10	12	30	2.9
Birch, black	3	6	8	9	48	2.0
Birch, yellow	3	5	6	7	11	1.7
Cherry, black	2	4	5	6	33	1.2
Cucumber	4	5	6	7	18	3.6
Hemlock	12	20	25	29	38	5.1
Maple, red	4	7	9	10	36	2.6
Oak, red and white	4	6	8	9	20	2.2
Pine, white	9	14	18	20	36	4.1

It is of interest to note that the average black cherry, *Prunus serotina* Ehrh., attained a height of one foot in two years while the average hemlock attained this height only at the age of twelve years.

AGE AND SIZE RELATIONSHIPS

It is generally known that there is a close relation between height and diameter, but, as Chapman ('24) indicates, this relationship may not be consistent for individual trees. Gates and Nichols ('30) found some correlation between age and diameter of hemlock and sugar maple, *Acer saccharum* Marshall, in a virgin Lake States stand. The available age, d.b.h. and height data obtained at Hearts Content were analyzed to determine if such relationships existed there. Unfortunately, a multiple correlation could not be attempted since the major portion of the age-d.b.h. data were from trees other than those from which the height-d.b.h. data were obtained. Consequently, age and height could not be correlated, but age and height were independently correlated with d.b.h. which was used as the independent variable in each case. The effect of this is shown (table II) in red maple, *Acer rubrum* L., whose height (which is not based on age) and diameter appear to increase although age does not when the larger diameters are attained. The data as presented in the table show what age or height a tree with a given diameter might have,

⁶ Hearts Content was divided into two areas by Lutz ('30) the hemlock consociation (70 per cent or more of the trees 10 inches and above in diameter being hemlock) on low ground, and the hemlock-beech association on higher ground.

TABLE II. Average ages and heights by diameter classes at Hearts Content¹

D.b.h. class inches	Hemlock				Beech			White Pine		Red Maple		Sweet Birch			Yellow Birch		White Oak		Cucumber	
	Age—years		Height—feet		Age—years		Ht. ft.	Age— years Assoc- iation	Ht. ft.	Age— years Assoc- iation	Ht. ft.	Age—years		Ht. ft.	Age— years Conso- ciation	Ht. ft.	Age— years Assoc- iation	Ht. ft.	Age— years Assoc- iation	
	Conso- ciation ²	Assoc- iation ²	Conso- ciation	Assoc- iation	Conso- ciation	Assoc- iation														
2.....	69	47	14	14	61	41	25		24	21	27	25	27	24	22	19	15	19		
4.....	104	69	25	24	88	61	42		46	36	28	37	43	40	40	34	24	34		
6.....	132	88	37	32	116	82	55		72	50	46	50	57	56	54	50	34	50		
8.....	160	104	49	42	148	102	64		102	62	71	62	66	76	64	64	48	64		
10.....	185	119	60	50	179	122	72		133	73	102	76	74	100	71	74	69	74		
12.....	209	131	71	58	213	142	78	156	163	80	134	91	79	127	77	134	106	81		
14.....	231	143	80	66	237	161	84	170	194	86	170	110	83	154	82	158	155	86		
16.....	252	153	88	74	254	180	90	183	224	91	198	139	87	172	86	182	175	90		
18.....	272	163	94	86	266	196	95	194	245	95	213	140	90	184	90	208	189	93		
20.....	292	172	99	86	272	207	99	203	253	98	222	140	92	193	94	233	199	96		
22.....	312	180	103	92	276	216	102	211	256	101	226	152	96	200	98	260	206	99		
24.....	330	188	106	96	278	219	104	218	258	104	228	154	97	204	102	288	211	101		
26.....	348	196	108	99	279	220	105	222	259	106	229	155	98			316	216	103		
28.....	366	203	111	102	280		106	226	259	108	230	156	99			344	220	106		
30.....	384	209	113	104		281	107	229	260	110	230	157				371	223	108		
32.....	402	216	114	106				232	260	112	230	158					226	110		
34.....	420	223	116	107				234	260	114	230	159					228	112		
36.....	436	229	117	108				236	261	115	230	160					230	114		
38.....	455	235	118	109				237	261											
40.....	472	240	119	110				238	261											
42.....	490	246	120	111				239												
44.....								240												
46.....																				
48.....																				
Statistical Measures																				
Number of Cases.....	37	73	31	68	33	107	121	58	68	99	23	53	98	47	73	20	58	82		
Range, d.b.h. inches.....	41.2	41.6	37.7	40.3	28.8	25.3	29.0	27.9	38.4	31.4	24.8	24.6	31.2	23.7	23.4	15.6	35.0	35.0		
Range, age, years.....	459	229			287	252	113	133	276	122	244	257	109	237	111	218	297			
Range, Height, Feet.....			99	106		28.3	8.0	26.0	38.8	9.0	10.1	13.8	6.2	27.1	6.8	36.3	25.4	116		
Standard Error ±.....	42.7	20.7	5.5	7.0	36.9	.835	.916	.496	.935	.972	.991	.975	.983	.931	.972	.720	.952	.988		
Correlation Index.....	.966	.953	.984	.979	.835	.916	.973	.496	.935	.972	.991	.975	.983	.931	.972	.720	.952	.988		

¹ From curved averages based on diameter breast high, hence shows probable age and height for a given d.b.h. and thus can not be used as a growth chart. Due to lack of height data (which could not be corrected) for all species except hemlock, the height data for both communities were used as a basis for a single curve for each species other than hemlock. The majority of these data were obtained in the hemlock-beech association. Only the curved averages for those cases where correlation was fair to good are presented. For example, although the range in years and d.b.h. of white pine in the consociation were respectively 71 years and 30.3 inches, no correlation between these variables could be obtained.

² Consociation (Conso-.) and Association (Assoc.) denote hemlock consociation and hemlock-beech association respectively.

not what height or diameter a tree of a given age has attained. The curves therefore can not be used to indicate growth, but their utility lies in approximating either age or height from a known diameter (Bruce, '25).

There were not sufficient data to permit the separation of heights, except for hemlock, upon a community (hemlock consociation and hemlock-beech association) basis. Indeed, enough heights for desirable height-d.b.h. curves could not be obtained for chestnut oak, *Quercus montana* Willd., white oak, red oak, *Quercus borealis maxima* (Marsh.) Ashe, chestnut, *Castanea dentata* (Marsh.) Bork., and black cherry.

Although high correlation indices for the age-d.b.h. relationship were obtained for the majority of the cases in table II, the curved averages should be used only when the limits of accuracy (shown by the relative high corresponding standard errors) are known. For example, the age of hemlock in the hemlock consociation changes directly as d.b.h. (high correlation index), but only in two-thirds of the cases will the age fall within ± 42.7 years of the estimate. Thus a hemlock 32 inches d.b.h. will, in two out of three cases, be from 359 to 445 years of age.

Little or no correlation existed between age and d.b.h. for red oak, chestnut, and black cherry. These species occurred either in a single age class or in several well defined age classes. Thus one is led to conclude that there may be a higher correlation between age and d.b.h. for species appearing in an all-aged form (considering the stand as a whole and not as localized groups) than for those species which are present in but several well defined age classes.

The low standard errors in the height-d.b.h. correlation, ranging from ± 5.4 feet for cucumber to ± 12.4 feet for white pine, indicate that height may be estimated from d.b.h. with a fair degree of accuracy at Hearts Content.

It is worthy of note that the average hemlock in the hemlock-beech association is much younger but little shorter than the average hemlock with the same diameter in the hemlock consociation. This indicates that growth conditions for hemlock may be better in the association. This is also true for the age-diameter relationship of beech, *Fagus grandifolia* Ehrh.

The height figures for the upper diameter classes present a clear picture of the crown levels of the various species when the area is viewed at a distance. The crowns of the pines tower from 20 to 40 feet above those of the nearest competing species, the hemlocks. Intermingled with the hemlock crowns are those of the hardwoods.

MAXIMUM AGES AND SIZES ATTAINED BY THE PRINCIPAL SPECIES

The maximum ages, diameters, and heights attained by the various species are listed in table III. The data given under "Maximum recorded" were obtained from the literature and from answers to letters of inquiry which were sent to the various forestry agencies located within the natural range

TABLE III. *Maximum diameters, ages, and heights of trees at Hearts Content*

Species	Hearts Content				Maximum recorded ¹		
	Situation	D.b.h. inches	Age years	Height feet	D.b.h. inches	Age years	Height feet
Hemlock.....		41.6 ²	492 ²	123 ²	62 ⁴	560+ ⁵	159 ⁴
Beech.....		29.0 ²	329 ²	118 ²	34+ ⁵	360 ⁷	
White pine.....		49.7 ²	330 ⁸	162 ²	54± ⁹	461 ¹⁰	170 ¹⁰
Red maple.....	B-H association.....	38.4	287	126			
Sweet birch.....		31.2 ²	266 ²	114 ²		330 ¹¹	
Yellow birch.....	H. consociation.....	24.0	247	118	38.0± ⁶	340 ¹²	
Chestnut oak.....	B-H association.....	26.4	376	100	34.0 ¹³		
White oak.....	B-H association.....	30.0	368	108	72.0± ¹⁴	400± ¹⁴	130 ¹⁴
Red oak.....	B-H association.....	38.0	294	128			
Cucumber magnolia.....	B-H association.....	35.0	300	120	38.8 ¹⁵		
Chestnut.....	B-H association.....	42.0	289	105	50.3 ⁹	300 ¹⁶	
Black cherry.....	B-H association.....	18.2	57	98	29.2 ¹⁵	85 ¹⁶	

¹ Maximum attained by species elsewhere than at Hearts Content. There are probably records of which the writer has no knowledge, which give greater maxima than those given here.

² Hemlock consociation.

³ Beech-hemlock association.

⁴ Pennsylvania. Prentiss, Albey and Edward M. Griffith, 1908. The hemlock; its history, biology, and economy. Unpublished manuscript.

⁵ Wetmore, Pa. (16 miles east of Hearts Content) Authority, Pennsylvania Forest School and Allegheny Forest Experiment Station.

⁶ Colebrook Forest, Conn. Dr. G. E. Nichols, 1913. The Vegetation of Connecticut. II Virgin Forests, Torrey—Vol. 13, pp. 199-215.

⁷ Near Tiona Station, Pennsylvania, 9 miles northeast of Hearts Content. Authority, Allegheny Forest Experiment Station.

⁸ Reported by H. J. Lutz and A. L. McComb, situation not known. The oldest white pine in a known location was an individual 295 years of age in the hemlock consociation.

⁹ Location not known. Authority, Professor Cheyney, University of Minnesota.

¹⁰ Michigan. Authority, V. M. Spaulding, 1899. The White Pine, U. S. Dept. Agr. Div. Forestry Bul. 22, p. 92.

¹¹ Northern Michigan. Authority, Lake States Forest Experiment Station.

¹² Franklin Co., N. Y. Authority, Northeastern Forest Experiment Station.

¹³ Graham Co., N. C. Authority, Chas. Mohr. 1900 Manuscript, U. S. Forest Service.

¹⁴ Kentucky, Anonymous, 1929. Oak. U. S. D. A. Forest Service, Mimeographed.

¹⁵ Wetmore, Pa. Authority, Allegheny Forest Experiment Station.

¹⁶ Southern Appalachian, E. H. Frothingham, 1919, manuscript, "Report on Site Study Reconnaissance, Southern Appalachians," U. S. Forest Service.

of these species. Only known ages and sizes are recorded here; estimates were not given consideration. No doubt there are records of older and larger trees than those listed here of which the writer has no knowledge. The figures given for each species do not necessarily represent those for a single tree. For example, the figures for hemlock at Hearts Content represent three trees, while those for cucumber in the same community are for one tree.

At Hearts Content, the largest diameters for all species, other than beech, white pine, sweet birch, *Betula lenta* L., and yellow birch, *Betula lutea* Michx., were attained by individuals living in the hemlock-beech association. The exceptions lived in the hemlock consociation. The oldest individuals of hemlock, beech, and yellow birch occurred in the consociation, while the oldest

of the other species occurred in the association.⁷ The greatest heights for hemlock, white pine, and yellow birch were attained by individuals living in the association.

The largest tree at Hearts Content was a white pine with a d.b.h. of 49.7 inches. The species having a maximum diameter smaller than that of any other species was black cherry with a d.b.h. of 18.2 inches. The maximum age for this species, however, was only 57 years. Larger and older black cherries may have existed in the locality, although no evidence of such existence now remains.

The oldest tree was a hemlock of 492 years which grew in the consociation. White pine was the tallest species present, the tallest tree being 162 feet. Black cherry and chestnut oak were the shortest species, their maximum heights being respectively 98 and 100 feet.

Although some of the trees at Hearts Content approach the known maximum age or size attained by that species, others do not. Hemlock, beech, white pine, yellow birch, and chestnut are younger here than at other places in their range. Since neither hemlock nor beech in the hemlock consociation have attained their known age or size, the community may not have attained the climax stage of succession at this time. One must consider, however, that site quality determines growth and that size, not age, may determine the life cycle of a tree (Chapman, '24).

SUMMARY

The ages, heights, and diameters breast high of some 800 trees of the principal species were secured in a virgin forest in northwestern Pennsylvania for a study of the relationships between d.b.h., age and height.

Although good correlation exists between age and d.b.h. for the major species, the dispersion of the data about the curved averages is too great to allow accurate estimation of age based on d.b.h. there.

High correlation and low standard errors for the height-d.b.h. curves permit estimation of height from d.b.h. with a fair degree of accuracy.

Although some of the species at Hearts Content approach their known maximum age or size the majority are younger and smaller than the maximum attained elsewhere within the range of the given species.

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⁷ The location of the oldest pine reported by H. J. Lutz and A. L. McComb is not known. The next oldest pine occurred in the hemlock consociation.

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SEASONAL GONADAL CYCLE OF THE ENGLISH SPARROW, *PASSER DOMESTICUS* (L.)¹

CHRISTIA ALLENDER

University of Oklahoma

Data on the seasonal gonadal activity of the English sparrow, *Passer domesticus* (L.), were collected during 1932 and 1933 in order to make a comparison with those given for other birds, especially the junco, *Junco hyemalis* (L.) (Rowan, '24-'29), and the European starling, *Sturnus vulgaris* L. (Bissonnette, '30-'33). The problem was suggested by Dr. A. Richards of the University of Oklahoma, to whom the writer is indebted for help.

LITERATURE

Etzold ('91) studied the development of the testes of the sparrow, *Fringilla domestica* L. (= *Passer domesticus* (L.)). He found a gradual increase in size and weight. The volume increased to three hundred times that of the resting condition, the diameter of the tubules to ten times, and the length sixteen times.

Loisel ('00-'02) made a similar study of the same species in France. He found that the sexual cycle began in January and that the size of the testes increased from one-half millimeter in length to twelve and a half by the end of April, and seventeen the last of May. Spermatozoa first appeared in the tubules about the middle or the end of March, when the testes attained the length of seven or eight millimeters.

Rowan ('24-'29) found that by increasing or decreasing the length of daylight periods, he could modify the sexual cycle accordingly. He induced sexual activity in the midst of winter by increasing the period of illumination and caused an inhibition of gonadal growth after spermatogenetic activity had begun by decreasing it. He found that the gonads of the junco could be held in a condition of partial regression for a month or more by holding the exposure to light constant. He also induced sexual activity by extending the period of daily exercise, without added light. Consequently he concluded that the increased daylight period affords a longer day for exercise, thereby bringing about sexual activity.

Bissonnette ('30-'33), working with the European starling, "found that the state of activity of the testes (and ovaries, as judged by gross inspection) could be modified at will, in either direction, within the limits of the natural

¹ Contributions from the Zoology Laboratory, University of Oklahoma, Second Series, No. 126.

changes by increasing or decreasing the daily periods of illumination." An electric light of fifty or sixty watts, added for four to six hours after dark, induced spermatogenesis in six weeks any time from December to April, while controls, without added light remained in the winter condition. Increased length of daily exercise period without added light was "decidedly inhibitory" to gonadal development, and caused increased pigmentation in the testes.

According to his experiments, diet plays a very important part in gonadal activity. With a diet short in proteins, fats, and vitamins, even red light of proven potency did not induce spermatogenesis. He thought that the lack of vitamins, which are essential to the normal function of reproduction, might be the reason for the failure to produce spermatogenesis.

Cole ('33) showed that increased daylight periods induced sexual activity in both male and female mourning doves one to two months earlier than normal.

The sexual activity of the English sparrow occurs somewhat earlier than that of the species discussed above and extends to early summer.

MATERIAL

English sparrows were collected at intervals of one to two weeks from November, 1932, to November, 1933, in Norman, Oklahoma. Other methods of collecting were tried, but shooting with a short rifle and fine bird shot was found to be the most satisfactory way. The gonads were removed immediately, inspected, measured and fixed for cytological study. They were collected at nearly every hour during the day from daybreak to dark and a few were collected after dark from roosts.²

OBSERVATIONS

Testes collected during the months from September to December average 2 mm. in length. Proliferation begins the first of January and by the last of the month some testes are 5.5 mm. long. During February the fluctuation is great, varying from 4 to 8 mm. in birds taken the same day, and even though testes grow to greater size later, sexual activity begins about March first. Cytological study corroborates this and activities of the birds themselves are in agreement, for they may be found building, mating and incubating. Mature sperm were found the first of March, although the maximum size of testes was not attained until May. Mrs. Nice ('30) says that week old young have been found on March 20th.

² The data for these collections and those upon which the accompanying graph is based are not included in this paper, but are available for inspection in a thesis deposited in the library of the University of Oklahoma.

Reproductive activity lasts till the middle of July. During the entire time the length of testes varies, but it is thought that the variation is due to individual differences. For instance, on May 6th, 1933, two birds were taken. The left testis of one was 9.5 mm. in the longest diameter and 7 mm. in the shortest, while that of the other was 10 mm. by 7. Yet the sperm appeared, from sections and smears to be as abundant in one as the other. Young sparrows with lighter colored bills were eliminated.

By the last of July regression has set in. It takes place as quickly or more quickly than the proliferation, occupying a period of from a month to six weeks. On August 27th two birds were collected, the testes of which measured 1.5 mm. All taken after that until late December were 1.5 to 2.5 mm. in length. Cytological observation revealed that there was very little difference structurally.

COMPARISON OF THE SEXUAL CYCLE OF THE MALE JUNCO AND ENGLISH SPARROW

Rowan's observations revealed that the testes of the junco remain in the resting condition during the four winter months, November to February, at the minimum size, 0.5–0.6 mm. in diameter. Intra-gonadal changes begin in March. About April the first the juncos arrive in their northern home, immediately after which the testes undergo rapid proliferation and in six weeks, by the middle of May, the birds are mating and nesting. The testes attain a length of 6 to 8 mm.

The condition of the testes of the English sparrow at this latitude corresponds to that described by Rowan for the junco, except for the time of year at which it takes place. The testes begin to enlarge in January and nesting and mating is begun by the first of March. The testes of the sparrow are not as small as those of the junco in the resting condition, being 1.5 to 2.5 mm. in length, and they grow to much greater dimensions in the longer breeding season (11 mm.). The breeding season of the junco lasts from the middle of May to July, while that of the sparrow begins in early March and regression takes place in August.

DISCUSSION

The accompanying figure shows in graphic form the data as to testis length, length of daylight period and temperature. Rowan ('29) has shown that spermatogenesis may be induced independently of rising temperatures by increasing the daily period of illumination. It is interesting to note that there is very little correlation in this case between testis length and temperature. The gonadal growth begins almost simultaneously with the increase in daylight periods and before any marked rise in temperature. It increases very rapidly as the days lengthen until March 17, and then the curve ascends gradually to a maximum in mid June. It is of further interest that as the

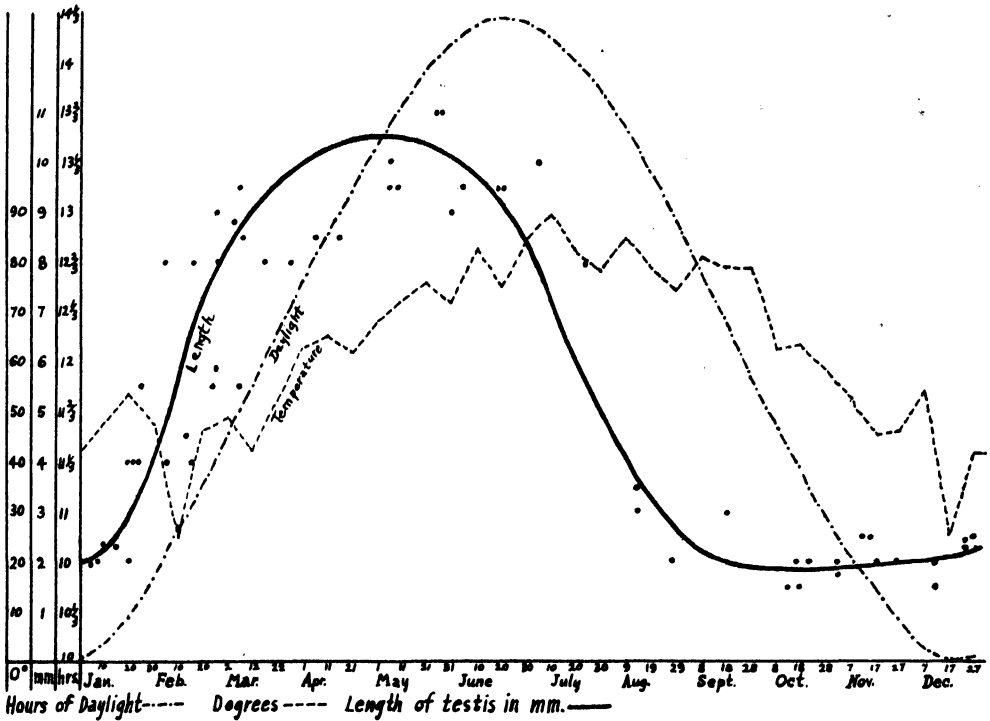


FIG. 1. The seasonal left testis length plotted with length of day and mean daily temperature for one year.

days begin to shorten after the summer solstice the testis length begins to decrease, and falls off rapidly as the days become shorter.

CONCLUSIONS

1. Gonadal activity in the English sparrow is at a minimum in this locality (Norman, Oklahoma) from the end of August to the last of December.

2. Beginning in January there is a period of rapid testis growth and development, culminating at about the time of the summer solstice.

3. This is followed by a period of rapid regression, ending when the resting condition is reached about September first.

4. The period of testis growth seems to coincide with that of increasing daylight and the period of regression with the period of decrease in the number of daylight hours.

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ATRIPLEX SEMIBACCATA AS INFLUENCED BY CERTAIN ENVIRONMENTAL CONDITIONS

DOLORES M. BULLOCK

University of Southern California

The Australian saltbush, *Atriplex semibaccata* R. Br., was introduced into the United States in 1887 by the California Experiment Station (Hall and Clements, '02) and has become established within an area designated by McKee ('19) as "the saltbush area." This is made up of certain arid and semi-arid portions of California and Arizona and islands off the southern California coast. Precipitation and temperature have been considered important factors in the distribution of the species. It is said to thrive most vigorously with a mean annual rainfall of about nine inches and a mean annual temperature of about 60° F. and to withstand the extremes of 10° F. and 118° F. The plant is noted for its tolerance of alkaline and saline soils and occurs generally in such lands throughout "the saltbush area." It is remarkable for its drought resistance, having been observed to endure less than five inches of rainfall without ill effects. *Atriplex semibaccata* is not tolerant of great quantities of moisture; and it has been noted that the species does not occur where the mean annual rainfall exceeds twenty-two inches.

This saltbush has proved of some value as a forage plant (Shinn, '99, Jaffa, '94), and the removal of the aerial parts by grazing or harvesting decreases the amount of saline and alkaline salts in the soil (Hilgard, '11). As a soil binder it is particularly efficient. Because of its salt content and succulence it is slow burning and has been planted by the California Forest Experiment Station as a cover on firebreaks where invasion of the annual grasses constitutes a serious fire hazard during the dry season.

The distribution of the species, its plasticity, nutrient value, and tolerance of drought and of alkaline and saline soils have been noted by various authors (Jaffa, '94; Shinn, '99; Hall and Clements, '02; Bedwell and Wooton, '25; Eaton, '27; and Wood, '34). Little study has been made, however, of the responses of the plant in habit and structure to variation in its environmental conditions.

PROCEDURE

Several stations were established near San Pedro, California. To determine differences in some of the environmental factors raingauges, Livingston spherical white cup atmometers, and maximum-minimum thermometers were set up at three principal locations which were situated successively inland from a rocky beach to a point three miles distant in the Palos Verdes Hills. Soil

moisture was determined weekly at each station and salinity during periods of drought and soon after precipitations. A mechanical analysis of soil at each site was made by the use of soil pans.

Growth figures were calculated bimonthly by a method similar to that used by Clements and Goldsmith ('24) with grasses. In the present study the length of the leaf, including the petiole, was multiplied by the breadth of the blade at its widest point. Bimonthly examinations were made of cross sections of leaves and measurements of their various tissues recorded. The water content was tested several times during the latter part of the investigation which extended from November, 1933, until late in May, 1934.

HABITAT AND PLANT DIFFERENCES

Nearest the ocean climatic conditions were most xeric, precipitation being less and evaporation, maximum temperatures, and range in temperature greater than farther inland. Three stations were established here, and though climatic conditions were approximately uniform, records of soil moisture and salinity showed that significant edaphic differences existed.

The first station, 1a, was situated on a ledge overhanging the beach and received the salt spray at high tide (fig. 1). Here the soil was a medium



FIG. 1. Coastal location. *Atriplex semibaccata* overhanging ledge at station 1a.

coarse sand with a high percentage of coarse gravel. Soil moisture was favorable throughout, but high salinity was evident (table I). Dense mats of the plants suggested large individuals of recumbent habit. Detailed observation, however, revealed many small individuals growing in close proximity. Lower branches only were prostrate, the majority being erect (table II). Foliage was markedly succulent and yellowed, and a large number of dead leaves were noticeable. Tables I, II, III, and IV supply further details on plant differences.

TABLE I. *Soil moisture,¹ salinity,² and some root characteristics*

Sta.	Percentage of soil		General root characteristics	
	Moisture	Salinity	Tap roots	Laterals
1a	19.4	4.00	Av. length 90 cm., small diameter	Small, rare
1b	17.1	1.20	Av. length 130 cm., deeply penetrating	Abundant
1c	21.3	1.60	Av. length 109 cm., small diameter	Small, occasional
2a	27.6	0.45	Av. length 150 cm.	Abundant, large, wide spreading
2b	18.3	0.90	Av. length 190 cm., deeply penetrating	Abundant, large, wide spreading
3	22.1	0.54	Av. length 140 cm.	Abundant, large, wide spreading

¹ Weekly mean, percentage on dry weight.² An average of all determinations.TABLE II. *Relative dryness¹ and some stem characteristics*

Sta.	Rank ²	Nature of stems	Prevailing position	General concentration of foliage
1a	3	Moderately woody	Mainly vertical	Terminal portions
1b	1	Markedly woody	Markedly vertical	Terminal portions
1c	4	Moderately woody	Mainly vertical	Terminal portions
2a	6	Comparatively herbaceous	Mainly prostrate	Distributed from base to tip
2b	2	Woody	Markedly vertical	Terminal portions
3	5	Moderately woody	Prostrate bases and vertical tips	Terminal portions more than toward base

¹ Soil moisture and evaporating power of the air are factors considered in the term "dryness."² Stations are ranked from the most xeric to the most mesic.TABLE III. *General characteristics of leaves*

Sta.	Prevailing shape			Color	Growth fig.		Increment of growth
	Contour	Apex	Margin		Nov.	May	
1a	Widely ovate	Obtuse	Entire	Yellowish	50	224	174
1b	Lanceolate	Acute	Widely dentate	Lt. green	50	150	100
1c	Ovate	Obtuse	Entire	Yellowish	50	225	175
2a	Long ovate	Obtuse	Entire	Dk. green	86	330	244
2b	Lanceolate	Acute	Widely dentate	Lt. green	80	218	138
3	No prevailing outline			Md. green	85	245	160

TABLE IV. *Structural characteristics of leaves*

Sta.	General arrangement of tissues	Amt. of palisade vs. aqueous tissue	Width of epidermis microns	Water content per cent	Width of x sect. microns
1a	Compact	Great preponderance of aqueous	25	329	367
1b	Compact	Preponderance of palisade	23	173	264
1c	Considerable inter-cellular space	Preponderance of aqueous	40	197	392
2a	Large amt. of inter-cellular space	Present in equal amounts	22	194	302
2b	Compact	Preponderance of palisade	23	233	274
3	Considerable inter-cellular space	Slightly more of aqueous	24	203	329

The second station of the coastal location, 1b, was less than 100 yards from the ledge station and situated in a shallow ravine midway up the side of a steep cliff (fig. 1). Here soil texture was extremely coarse with a high percentage of fine gravel in addition to an abundance of the larger rock particles. This probably explained the great fluctuation in the amounts of water in the surface layers. Although the mean weekly moisture content seems reasonably favorable (table I), it was far drier than this mean percentage indicates. Salinity was high according to most authorities. Plants were large, wide spreading, and many branched, with stems more woody and of greater diameter than those of any other site.

The third coastal station, 1c, was located at the summit of the cliff. The soil was of coarse texture but lacked the high percentages of gravel found at the ledge and mid-cliff stations below. Root and shoot development seemed inhibited here as at the ledge station though to a lesser degree, and plants were generally similar to those of 1a. At each of these stations the immature berry-like fruits were noted in April when there was no evidence of those structures elsewhere.

About one mile inland a range of low hills marked the beginning of a belt of foothills. Ravines cut by drainage waters presented habitats of comparatively mesic nature. One of these was chosen for a second group of stations, the first at the bottom of a ravine and the second at the summit of its east slope (fig. 2). Instruments were set up at the former while edaphic conditions only were measured at the latter.

At the ravine bottom station, 2a, evaporation rates, maximum temperatures, and the range in temperature were lowest, and soil moisture was highest as compared with other sites. Salinity was accordingly less than at the drier habitats (table I). In addition to the dominant saltbush several other species were present, while at other stations the stands of *Atriplex semibaccata* were rarely invaded. In this sheltered location large individuals formed thick



FIG. 2. Ravine location. Stations 2a and 2b.

verdant mats carpeting the floor and extending up the sides of the ravine for five or six feet. Stems of these plants were of greater length and possessed longer internodes than those at other stations; leaves were noticeably larger.

At station 2b conditions were far more xeric than at the ravine bottom. The coarse textured soil contained a high percentage of gravel, and the rocky substratum was but a few inches from the soil surface. Soil moisture seemed similar to that at the mid-cliff station; salinity was considerably less. Plants were wide spreading and occurred singly in mats of from four to six feet in diameter. With the exception of their larger size, individuals here closely resembled those of the mid-cliff station.

At the location farthest inland, station 3, an abundant growth of *Atriplex semibaccata* occurred in a field three miles distant from the coast. Environmental conditions were approximately intermediate between those of the dry coastal and ravine summit sites on the one hand and the ravine bottom on the other. Minimum temperatures were lower than at other locations, and the amount of precipitation was somewhat greater. The fine textured adobe soil was markedly different from those of previously discussed habitats, and salinity was high considering the location of the station. Plants were many branched and generally formed rounded mats of about four feet in diameter. Where individuals exceeded this size it was frequently found that many of the aerial shoots ascended from lateral roots rather than from the base of the plant.

DISCUSSION

Where salinity averaged 1.2 per cent and less, extensive development of aerial and underground parts occurred. In relation to the size of the shoot systems, however, the roots in the drier soils penetrated more deeply and possessed more laterals than did those in soils of more favorable moisture con-

tent. Lignification of stems and their vertical position appeared correlated with moisture relations, the most upright stems characterizing the most xeric habitat, while the reverse was true at the most mesic station. Length of internodes and concentration of leaves to the terminal portions of stems also varied with moisture conditions, the longest internodes and widest distribution of leaves along the stem occurring at the moist ravine bottom station, while the shortest internodes and the most marked restriction of foliage to terminal parts was evident at the dry mid-cliff station. Leaf size and the increment of growth was greatest at the most mesic station, and there leaves contained the largest amount of intercellular space or the least degree of compactness. It was also noted that the smallest leaves with the most compact arrangement of tissues occurred at the most xeric site where the increment of growth was least. The epidermis was thin at all stations with the exception of the cliff summit habitat (table IV) where the leaf contained a considerable amount of intercellular space and was subject to high rates of evaporation, high maximum temperatures, and the greatest range in temperature.

In a soil of higher sodium chloride content than has hitherto been reported within the tolerance of the species, an abundant growth of *Atriplex semibaccata* occurred; but both root and shoot development were definitely impeded by concentrations of 1.6 per cent and above. The presence of many yellowed and dead leaves seemed to indicate that chlorophyll formation was adversely affected, and that plants were short-lived in soils of high salinity. Concentrations averaging 1.6 per cent and above appeared to stimulate the development of water storage tissue as leaves of the two more saline stations contained more aqueous than palisade tissue; and the amount at the excessively saline site was markedly greater than that at the station of secondary salinity. Where the percentage averaged less than 1.6 the proportion of palisade to water storage tissue was more easily correlated with moisture relations than with other conditions. Where moisture relations were most favorable, nearly equal amounts of those tissues occurred; but in drier habitats the palisade definitely overbalanced the amount of aqueous.

Leaf thickness and moisture content could not be correlated with any particular set of factors; nor could it be established that these characteristics were related. The thicker leaves, however, occurred at the two more saline coastal stations, the thicker of these being associated with the soil of greater moisture content rather than with that of higher salinity. Those of the inland and ravine bottom sites followed in descending order, while leaves at the dry mid-cliff and ravine summit stations were very thin. Leaf shape and thickness were generally associated, the thicker leaves being ovate with entire margins, while thin leaves tended to be lanceolate with widely dentate margins.

The writer has sincerely appreciated the guidance of Dr. H. de Forest of the University of Southern California in the conduct of this investigation and his aid in the preparation of the manuscript. She is also grateful to Dr. C. J.

Kraebel of the California Forest Experiment Station for his helpful suggestions.

SUMMARY

Atriplex semibaccata R. Br., an Australian saltbush, was investigated in several habitats near the coast in southern California. Modifications of habit and leaf structure were noted and associated with differences in certain of the environmental conditions, particularly with respect to the influences of temperature, evaporation, soil moisture, and salinity.

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SOME OBSERVATIONS ON THE REACTION OF PINE SEEDLINGS TO SHADE

G. A. PEARSON

Southwestern Forest and Range Experiment Station

Light in its relation to tree growth is a subject of never ceasing interest to foresters. Long before scientific studies had been made of the reaction of plants to light and shade, silviculturists had learned to recognize sunlight as one of the main instruments of their craft. Early foresters distinguished between direct, reflected, diffuse, overhead and side light. They classified trees as light-demanding or shade-enduring, and listed species in the order of relative "tolerance" or ability to function in shade.

Many investigators have studied the light requirements of trees. In recent years, attempts have been made to give quantitative expression to these requirements in the units of some form or other of light measuring apparatus. Most of these investigations have been made in the laboratory and have concerned themselves primarily with photosynthesis, it being found generally that very low light intensities are adequate for this process. Notable exceptions are the works of Gast ('30) and Shirley ('32), who found the best development of coniferous trees in light intensities approaching full sunlight. As a rule, scant attention has been given to the influence of light on tree form. Korstian ('25) found that Douglas fir and Engelmann spruce seedlings in the nursery attained the best development in half shade but became too slender when the light was reduced to 25 per cent. Relatively recent investigations have distinguished between light and moisture effects, but few have taken temperature into account. The importance of all of these factors has been discussed by the author ('29, '30) in previous articles. Clements and Long ('34), working with sunflower under outdoor conditions and using four degrees of sunlight (100, 32, 16 and 8 per cent), found that the greatest stem diameter and weight but not the greatest height growth were obtained where both sunlight and moisture were at a maximum. A reduction of sunlight to 32 per cent while retaining the highest soil moisture resulted in a marked decrease in stem diameter and weight but an increase in height.

The experiment here described was carried on in the nursery of the Fort Valley Experimental Forest, near Flagstaff, Arizona. It was begun in 1929 and is still in progress. Ponderosa pine, *Pinus ponderosa*, was the species used in the main experiment, although a few comparisons were made with spruce and Douglas fir.

OBJECT

The object of the experiment was to determine the effect of different degrees of sunlight upon survival, growth and form of ponderosa pine. By survival is meant not merely persistence through a few months, but the ability to carry on and develop normally through the seedling and sapling stages into the adult class. Form is important because it determines in large measure the ability to survive, and it determines even more than size the timber value of a tree. Too many investigators have used height growth alone as a criterion of favorable response to environmental factors. Rapid height growth is much to be desired in forest trees, but if the stem is not sufficiently sturdy it eventually falls of its own weight or under the burden of wind and snow. Trees growing in deficient sunlight tend to become too slender, while those exposed to intense sunlight develop too much in the opposite extreme.

METHOD

This experiment consists essentially of growing ponderosa pine under lath shades of different densities and in full sunlight. Plantings were made in 1929 and 1930, using both seed and 2-year-old nursery-grown transplants. The soil was a fertile sandy loam which had been under cultivation several years. Weeds were kept out consistently. Water was applied to the transplants two or three times immediately after planting, and then discontinued. The seeds were sown during the summer rainy season, and they germinated without being watered. Natural precipitation was ample at all times except for seedlings less than 2 years old which were watered occasionally in the early part of the summer and in the fall. Water supply was not a limiting factor nor was it allowed to become an appreciable variable. The shades were built of lath so placed as to intercept approximately 50 and 90 per cent of the sunlight, thus giving corresponding light intensities of 50 and 10 per cent. In view of the controversy surrounding methods of measuring light, and the fact that relative rather than exact light values were sought, no instrumental measurements were made. The shelters were 8 feet square and 4 feet high. Supporting framework reduced the light intensity somewhat below that indicated by the spacing of the lath.

The first planting was in May, 1929. In addition to the 50 and 10 per cent light intensities, a control plot in the open was planted. Nine 3-year-old transplants were spaced about 2 feet apart, leaving a margin of 2 feet around the inside of each shelter. Seeds were sown in July after the summer rains had started. Growth of the transplants in the dense shade began from 1 to 2 weeks later, and both shoots and leaves were weaker than in the half shade or full sunlight. In the half shade new growth appeared normal except that the shoots when fully grown were more slender than in the open. Germination began 2 or 3 days later in the half shade and about 10 days later in the dense shade than on the unshaded plot. Final germination was good in all plots.

During August and September, 1929, soil temperature was recorded daily at noon and 5 P.M. for a depth of 6 inches below the surface. The readings were consistently higher at 5-o'clock than at noon. Cloudy, rainy weather prevailed through August. The average 5-o'clock temperature during this month was 6.1° F. lower in half shade and 10.2° lower in dense shade than in full sunlight. In September, a month of less rainfall and more sunshine, the difference was greater but the general relation unchanged.

Although the plan aimed to maintain uniform soil moisture conditions in the several light intensities, it is evident that the shaded plots were favored by lower evaporation. The precipitation by months in 1929 was: June T., July 4.88, August 7.24, September 1.88, October 0.40. In the shelter of 10 per cent light intensity, the soil remained moist on the surface throughout the rainy period of July and August and well into the autumn. During succeeding years the amount of precipitation varied, but the July-August maximum which is characteristic of the region persisted. The soil below a depth of 6 inches was so evidently well supplied with moisture on all the plots even in June and October that soil moisture determinations would have had no significance.

By the end of the first season, marked differences were plainly noticeable in comparing the plants of the three light intensities. In the dense shade, the season's growth of stems and needles was distinctly less than in the half shade and full sunlight. The seedlings of July germination were much taller, more slender and of paler color in the dense shade than in the open. In the half shade both the seedlings and the transplants were similar to those in the open, but the seedlings were noticeably more slender. In late November, all the seedlings were mulched with pine needles placed on the sides but not over them. The transplants were not mulched. Shortly before the first heavy snowfall the overhead portion of the shades was removed, allowing the snow to imbed the plants. They were left in that condition until the snow disappeared in March, when the shades were replaced.

The first spring examination in April, 1930, revealed that all the plants, both transplants and seedlings, in the dense shade were dead. No casualties were found in the companion plots. In another series of plots 5 miles distant, seedlings in tall grass suffered much higher mortality than those where the grass had been clipped to 2 inches and 6 inches, or entirely removed. In both experiments rains through the autumn months followed by snow in January precluded any possibility of winter drought. The most plausible explanation is that low assimilation and food storage, due to the lowered insolation during the growing season, left the shaded plants in a poor condition to withstand the winter. Korstian ('25) has found that Douglas fir seedlings grown in shade have a lower concentration of cell sap than seedlings of the same species grown in full sunlight.

In 1930 the planting and sowing was repeated, substituting 20 per cent for 10 per cent light. Two of the 9 transplants failed to recover from the

shock of transplanting. The behavior of the remaining plants as to form, and the germination of seeds was essentially a repetition of the experience of 1929. Examinations in the spring of 1931 again revealed a loss in the dense shade, though in this instance only 3 out of the 7 transplants and about half of the young seedlings were actually dead. As in the previous winter, the half-shade and the control plot suffered no winter damage.

These experiences with winter killing are in line with observations on natural reproduction beginning in 1919. Earlier investigations had stressed the need for winter protection. Heavy losses in tall grass had been attributed to root competition, though light was recognized as a factor in the shade of trees. The present experiment points to overhead shade formed by tall grass as well as trees as distinctly detrimental to ponderosa pine seedlings. It also indicates that though light shade may not be injurious it is not needed if soil and moisture conditions are favorable.

In the spring of 1932, only 2 of the transplants in dense shade were alive. All the dead plants were replaced. In addition, several each of Douglas fir and blue spruce transplants were planted on all three plots. Seeds of Douglas fir and Engelmann spruce were sown in the two shelters. The pines in the dense shade have died year by year until in 1935 only 2 of the 1930 planting and 2 of the 1932 planting remained. The Douglas fir and spruce (both transplants and seedlings) are surviving in the dense shade as well as in the other two plots.

EFFECT OF SHADE ON FORM OF TREES

In the course of annual examinations, striking differences in form, size and general development became evident in the young pines. The outstanding features were slow growth, slender stems and needles, and general lack of vigor in the dense shade; apparently good height growth but subnormal diameter growth in the half shade (fig. 1) and vigorous, sturdy growth in full sunlight (fig. 2). Table I gives a comparison of the 1929 plantings in the two highest light classes with respect to diameter and height of stems, current height growth and length and weight of needles at the close of the growing season in 1933. Weights of the entire plants were not obtained because it was desired to continue the experiment.

Table I strikingly confirms the impression gained from observation that shade tends to make both stems and needles more slender than those grown in full sunlight. The slender appearance of the stems in shade is due directly to low diameter growth in proportion to height growth. Height growth is also reduced, but less so than diameter growth. These relationships are most evident in the seedlings, as would be expected from the fact that they have been subjected to different influences from the beginning of germination. After 5 years the contrast has become greater rather than less, indicating a cumulative effect. During the winter of 1933-34 several of the taller trees

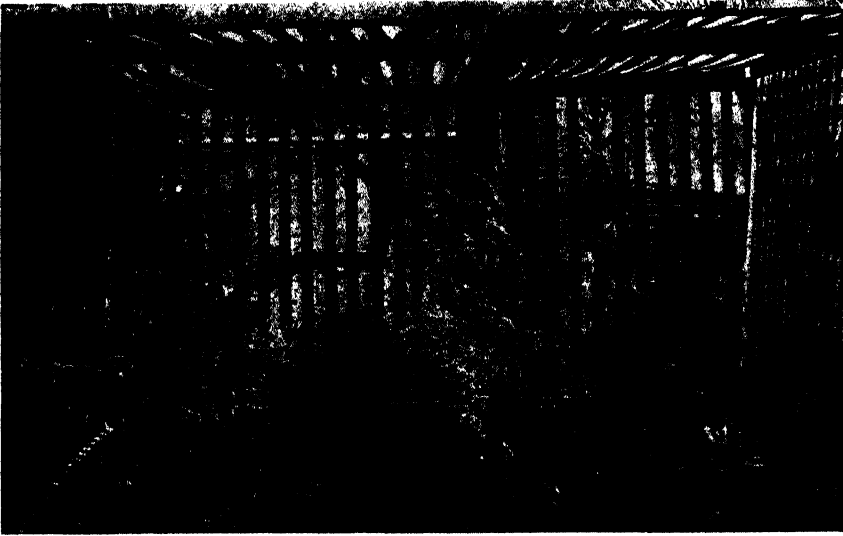


FIG. 1. Influence of shade on the form of pine seedlings. Slender stems with fine branches and needles in half shade.



FIG. 2. Influence of shade on the form of pine seedlings. Sturdy stems, with coarse branches and needles in full sunlight.

in the half-shade plot were bent over by snow to such extent that they had to be propped up the following spring. The overhead shade was not replaced because the tallest seedlings had reached the "ceiling."

None of the plants in dense shade are strictly comparable with those in the other two light intensities because the only survivors in dense shade (80 per cent) were planted 1 or 3 years later than those in full sunlight or half

TABLE I. *Comparison of ponderosa pine seedlings grown in sun and half shade, with respect to average dimensions of stem, current growth, and length and weight of needles, 1929 planting*

Year of measurement and class of plants	Diameter of stem				Total height		Height growth in 1933		Length of 1933 needles		Green wt. 1933 needles	
	Base		1933 leader									
	Full sun	Half shade	Full sun	Half shade	Full sun	Half shade	Full sun	Half shade	Full sun	Half shade	Full sun	Half shade
1932 Transplants Seedlings	2.35 .87	1.39 .37			61.5 25.4	57.9 16.5						
1933 Transplants Seedlings	3.04 1.13	1.75 .56	1.02	.66	85.9 43.9	80.8 27.9	28.4	24.9	16.0	15.7	.149	.108

Note: All measurements of diameter and height in cm. are the average of all plants. Length of needles is the average of three random measurements on each 1933 leader. Needle weights in gr. are the average of 54 needles, 9 from the 1933 leader of each plant.

shade. The two survivors of the 1930 planting measured at the end of 1933 only one third as much in height and one fourth as much in diameter as did the seedlings grown in full sunlight. An even greater contrast is noticeable in the length of branches and in the number, size and vigor of needles.

SIGNIFICANCE OF THE FINDINGS

The failure of the pines to survive in the dense shade points directly to deficient insolation, but not necessarily to deficient light for photosynthesis, as the sole cause. Obstructing the sun's rays decreases heat energy as well as light in the technical sense. The effect is not reflected in air temperature, as usually measured, but it is roughly measurable in soil temperature. Soil temperatures 6 inches below the surface were from 10 to 12 degrees higher in the open than under the close lath screen. About the same relation is found in comparing situations shaded by large pine trees with adjoining ones in nearly full sunlight. Pine seedlings do not survive where the shade of old trees persists through the greater portion of the day. But pines planted in full sunlight in the Engelmann spruce forest at 10,500 feet have behaved in a manner similar to that of the pines in dense shade in the pine forest at Fort Valley, 3000 feet lower. The mean maximum air temperature in the spruce during the four growing months, June, July, August and September, is 61° F. as compared with 77° F. in the pines. Corresponding soil temperatures at a depth of 1 foot are 43° and 65°. In a small nursery bed of pine seedlings grown from seed sown in 1918 in the spruce opening, the 4 survivors in 1927 were only 8 to 11 inches tall. Seedlings grown under similar conditions in the pine zone commonly attain this height in 3 or 4 years.

Douglas fir, blue spruce and Engelmann spruce planted at Fort Valley in 1931, both as seed and as transplants, in 20 per cent sunlight, where most of the pines died within a year, are all surviving, though somewhat abnormal in appearance. It is well known that all of these species exceed ponderosa pine in the capacity to function in low light intensity and low temperature. In the usual habitats of these four trees the lowest mean maximum temperatures for the growing season of June 1 to September 30 are: ponderosa pine 70°, Douglas fir 62°, blue spruce 60°, Engelmann spruce 57° (Pearson, '31).

As between half shade and full sunlight, the difference in form is most conspicuous, though the smaller diameter of the stems in half shade points unmistakably to lower wood production. The extremely slender form in half shade, in contrast with the coarse development in full sunlight, suggests that a light shade about midway between the two might prove advantageous. Removal of the top screen from the plot in half shade and leaving the side screens may accomplish an even better result. This is nature's method. The dominant individuals in sapling thickets receive nearly full sunlight from above, but are shaded on the sides. Isolated young trees growing in small open spaces surrounded by tall trees are subjected to somewhat similar conditions. In both instances the side shade promotes development of the long clean trunks prized by the lumberman and admired by the nature lover.

SUMMARY

Ponderosa pine seedlings were grown in a nursery for 5 years under uniformly favorable moisture conditions but under varying degrees of sunlight. Four grades of insolation, namely, full sunlight, approximately 50, 20 and 10 per cent of full sunlight were compared. All plants in the lowest light intensity died during the first winter. All but two of those in 20 per cent light died during the 5-year period and the survivors were much smaller and more slender than those in full sunlight or half shade. The plants in half shade made slightly less height growth and only about half the diameter growth of those in full sunlight.

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RELATIVE HUMIDITY OR VAPOR PRESSURE DEFICIT

DONALD B. ANDERSON

The University of North Carolina, Raleigh

Being well aware of the profound importance of evaporation as a factor affecting plants and animals, biologists are careful to regulate or observe it in experimental work. Evaporation is a dynamic process and represents the net difference between the number of water molecules leaving a surface and the number returning to the surface during some unit of time. It is frequently difficult or impossible to control the number of water molecules leaving the surface of living tissues, but it is often possible for us to control the rate at which water molecules return to these surfaces from the surrounding atmosphere. This is usually attempted by regulating the relative humidity of the atmosphere. Biologists sometimes fail to realize that identical relative humidity values do not indicate identical atmospheric moisture conditions unless the temperature is also the same. If identical atmospheric moisture conditions are desired at different temperatures it is necessary to maintain different relative humidities. Although this fact has been pointed out earlier by a number of different workers (cf. Bolas, '26; Braun-Blanquet, '32; Day, '17; Imms, '31) it seems worth emphasizing here again. It is the purpose of this paper to show graphically some of the significant relations between relative humidity values and atmospheric moisture conditions and to point out some of the advantages of using vapor pressure deficits rather than relative humidities in measuring the effect of atmospheric moisture conditions upon living organisms.

It is important to realize that, when considered independently of other factors, the actual amount of water vapor present in the air has little, if any influence upon evaporation (Day, '17). The dryness or wetness of a climate is not correlated with the amount of water vapor in the atmosphere. The very "dry" atmosphere of Death Valley, California, probably the most arid region in the United States, contains on the average in July almost exactly the same amount of water vapor per unit of volume as does the "moist" atmosphere of Duluth, Minnesota, at the same time of the year. Braun-Blanquet ('32) cites an equally striking illustration of the lack of correlation between the "dryness" of the atmosphere and its moisture content by stating that the arid deserts of Morocco have a relative humidity of 90 per cent in the summer months. Very obviously the importance of atmospheric moisture as a factor affecting the rate of evaporation lies not in the absolute quantity of moisture present but in the relation between the amount present and the amount that could exist under the same conditions without condensation.

This important relation between the actual water vapor content of the atmosphere and the amount capable of existing at saturation under the same conditions may be expressed in terms of relative humidity or of saturation deficit. The relative humidity is a measurement of the actual moisture content of the atmosphere expressed as the percentage of the amount that could exist under the same conditions without condensation. It is, therefore, not a direct measure of any absolute quantity of water vapor but merely a ratio between two known values. Since the capacity of space to hold water vapor increases rapidly with an increase in the temperature, approximately doubling for every rise of 20° F., it is clear that the same relative humidity at different temperatures indicates very different atmospheric moisture conditions. An atmosphere 70 per cent saturated at 60° F., will contain much less water vapor than at atmosphere 70 per cent saturated at 80° F. What is more significant, the capacity of space to hold additional water vapor is much less in the first case than in the second. Evaporation will therefore occur more rapidly from a moist surface under the same conditions into an atmosphere with a relative humidity of 70 per cent at 80° F. than into an atmosphere with the same relative humidity at 60° F. That this difference is not a direct effect of temperature alone is clear from the absence of any correlation between temperature and evaporation (Rohwer, '31). A statement of the relative humidity of the atmosphere alone gives no indication of the atmospheric moisture conditions. An atmosphere with a relative humidity of 90 per cent may be very "dry" (when the temperature is high) or it may be very "wet" (when the temperature is low). Conversely a relative humidity of 30 per cent may indicate "dryness" at high temperatures or "wetness" at low temperatures.

The term saturation deficit has been used with two distinctly different meanings. Sayre ('20) uses the term to refer to the difference between the relative humidity and saturation expressed in per cent (100 per cent minus relative humidity). A relative humidity of 70 per cent is equivalent in this sense to a saturation deficit of 30 per cent. The term is more commonly used to express the difference between the actual amount of water vapor present and the amount present at the saturation point at the same temperature. This difference is expressed either in units of pressure (inches or mm. of Hg) or in units of weight (grains per cu. foot or grams per cu. meter). To avoid confusion it is desirable to have a term free from any possible misinterpretation. Since the vapor pressure is a measure of the quantity of water vapor present, temperature being constant, the vapor pressure deficit seems an entirely satisfactory term to express the mathematical difference between the amount of water vapor actually present and the amount that could exist without condensation at the same temperature. The vapor pressure deficit gives at once a very direct indication of the atmospheric moisture conditions independently of the temperature. A vapor pressure deficit of 2 mm. indicates at once the gradient between the amount of moisture in the

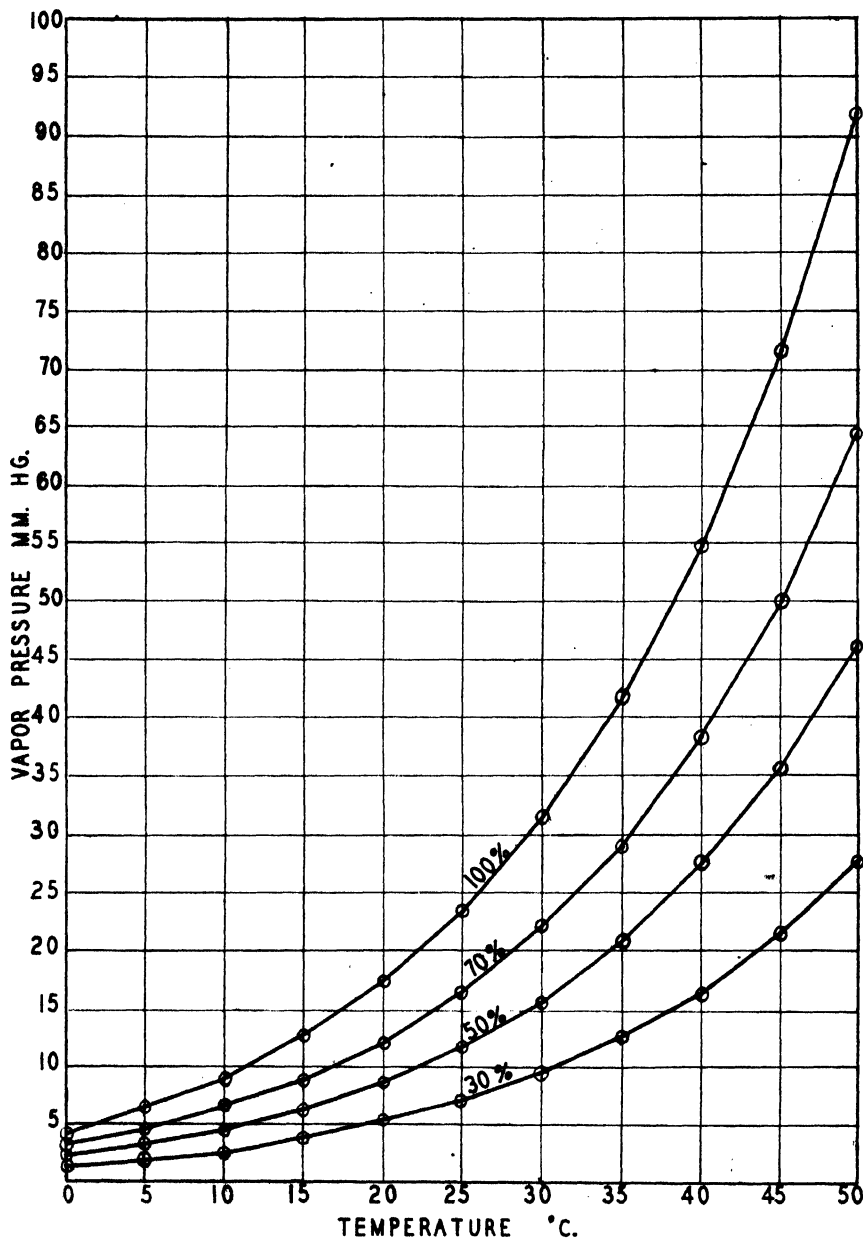


FIG. 1. The amount of water vapor present in the atmosphere at definite relative humidities over a range of temperatures.

atmosphere and the saturation point and at any temperature indicates a similar rate of evaporation. *E. Lindberg*

Figure 1 shows the actual amount of water vapor present in the atmosphere at definite relative humidities over a range of temperatures. Since the capacity of space to hold water increases greatly with the temperature the actual amount of water present at any specific relative humidity must vary

with a change in temperature. The capacity of space to hold water likewise changes. The vertical distance between the 100 per cent line and any of the relative humidity curves indicates the vapor pressure deficit at the temperature indicated. It is clear that the vapor pressure deficit undergoes marked variations with temperature changes when the relative humidity is constant. A relative humidity of 30 per cent at 10° C. is equivalent to a vapor pressure deficit of 6.45 mm. while the relative humidity of 30 per cent at 50° C. is equivalent to a vapor pressure deficit of 64.76 mm. In other words evaporation from moist surfaces exposed to the air with a relative humidity of 30 per cent will be ten times as rapid when the air temperature is 50° C. as when it is 10° C.

The rate at which water vapor molecules will return to any exposed surface will depend upon the capacity of space to hold water. If we maintain a constant difference between the amount of water in the atmosphere and the water holding capacity at saturation we will maintain a condition under which water vapor molecules will return to an exposed surface in equal numbers. The problem becomes one of keeping a constant difference between the actual amount of water vapor present and the capacity of the space to hold water vapor at the same temperature. To keep evaporation constant we must maintain a constant vapor pressure deficit.

The significant differences between relative humidity and vapor pressure deficit measurements may be indicated in a different way. Figure 2 shows the variation in relative humidity necessary to maintain the vapor pressure deficit at a constant value when the temperature is varied. To maintain the same vapor pressure deficit at the higher temperatures the relative humidity must be increased and the amount of the increase is shown by the position of the curves at the temperatures concerned. Both figures are based upon the data from Hodgman ('34).

The strain under which an organism is placed in maintaining a water balance during temperature changes is much more clearly shown by noting the vapor pressure deficit than by recording the relative humidity. The vapor pressure deficit undergoes a much greater variation than does the relative humidity during temperature changes (Day, '17). This fact is illustrated by the following data:

Air temp. ° C.	Relative humidity	Vapor pressure in mm. Hg	Vapor pressure deficit in mmg. Hg
20°	70%	12.28	5.26
30°	38.6%	12.28	19.54

A rise of temperature from 20° C. to 30° C., assuming no change in the vapor pressure of the atmosphere, brings a change of less than 32 per cent in the relative humidity but a variation of more than 370 per cent in the vapor pressure deficit.

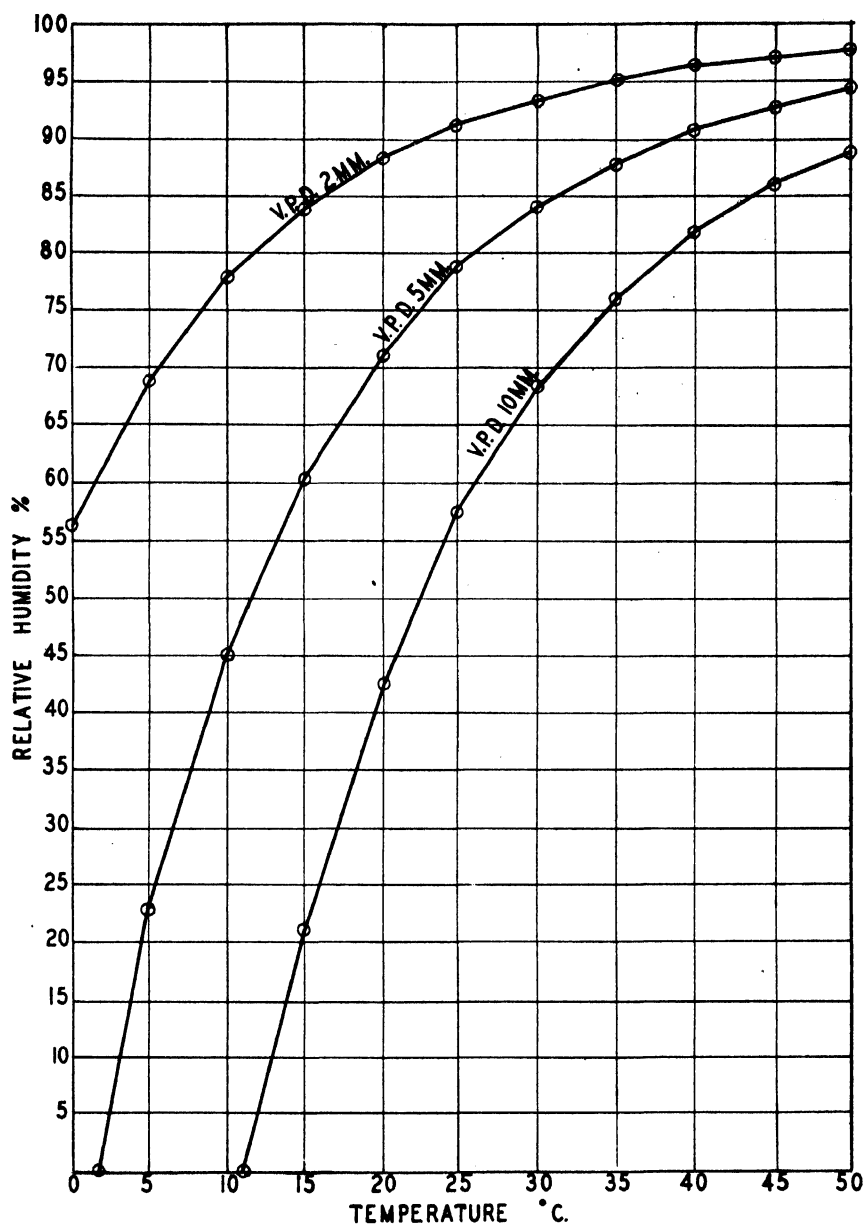


FIG. 2. The relation between relative humidity and vapor pressure deficit at different temperatures.

From these data it seems evident that relative humidity measurements are less satisfactory in biological work as indicators of the atmospheric factors influencing evaporation than are measurements of vapor pressure deficits. The advantages of vapor pressure deficit measurements over relative humidity measurements may be summarized briefly as follows:

1. The vapor pressure deficit is a much more sensitive indicator of the

water vapor conditions of the atmosphere and undergoes greater variations for temperature changes than does the relative humidity.

2. The fact that two different areas have the same relative humidity does not imply a similarity in the water vapor conditions of the atmosphere unless temperatures are also identical. Areas having the same vapor pressure deficits on the other hand do influence evaporation rates in the same way whether temperatures are identical or not.

3. Relative humidity alone gives no indication of the rate of evaporation while the vapor pressure deficit alone does give an indication of the evaporation rates.

For these reasons it is desirable that vapor pressure deficits be recorded in experimental work with organisms rather than relative humidities.

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THE RELATION OF SUCCESSIONAL DEVELOPMENT TO THE SILVICULTURE OF FOREST BURN COMMUNITIES IN SOUTHERN NEW YORK¹

H. G. WILM

California Forest and Range Experiment Station

The effect of fire is to set back the progress of forest succession into one of its earlier stages; in severe conflagrations, perhaps even to denude a site completely, thus starting successional processes practically anew. In the handling of a burned forest area it is desirable that the silviculturist learn the approximate period of time required for such a secondary succession to proceed naturally to its climax, and to ascertain whether it is feasible to hasten or alter its progress so as to obtain the desired commercial stand earlier than it would occur naturally.

This study was intended to provide an answer to the above questions for a typical burned-over and partly regenerated forest area in south central New York. The object was to determine: (1) the present stage or stages in succession of the existing secondary communities, and their plant indicators, if such exist; (2) the trend of succession in these communities, and the character of the climax toward which they are developing; and (3) where successional progress seems unsatisfactory or where it might be hastened, to investigate the possibility of artificially introducing forest stands of desirable character, or of otherwise favorably altering the course of succession.

LITERATURE

A review of the available publications on secondary forest succession, plant indicators, and ecological methods gives rise to a number of conclusions:

1. The normal stages in a secondary succession after fire in the northern hardwoods region are: (*a*) xerophytic herbs and low shrubs, (*b*) a raspberry-blackberry community, followed soon by (*c*) aspen, pin cherry, and other intolerant or light-demanding trees, with a more or less dense ground cover of shrubs and herbs, (*d*) a mixed hardwood association of more tolerant trees, with a fairly dense canopy and a corresponding decrease in the amount of subordinate vegetation, and (*e*) the climatic climax, which in this region is doubtless a beech-maple association (Bergman and Stallard, '16; Clements, '26; Gleason, '18; Lutz, '28; and Skutch, '29).

2. It is generally inadvisable, in intermediate forest communities, to attempt to hasten the return of a commercial forest by the artificial introduction

¹ Summary of a thesis presented for the Ph.D. degree, Cornell University, June, 1932.

of pure stands of conifers, for several reasons: the high cost of establishment and maintenance of such stands (Lutz, '28); the difficulty of preserving them against the invasion of natural communities (Chrysler, '05, Lutz, '28); and the reduction in soil fertility which has been said to accompany the development of pure coniferous plantations on hardwood sites (Fisher, '28). Intermediate communities are best handled by allowing a more or less natural progression to the climax, assisting it wherever possible by improvement cuttings (Lutz, '28).

3. As to methods for studying vegetation, the strip method of sampling appears to be satisfactory for relatively large woody vegetation. Quadrats are best adapted to smaller vegetation because of their ease of establishment and on account of their fundamental relation to the determination of frequency (Raunkiaer, '08; Smith, '13; Fuller and Bakke, '18; Gleason, '20). The best size of quadrat for use in the analysis of sparse to moderately dense herbaceous and shrub communities is probably a square meter (Gleason, '20; Lutz, '28; Stallard, '29). The number of quadrats employed depends on the size and degree of homogeneity of the community, but should generally be at least a hundred (Gleason, '18). The criteria which best describe the importance of any species in a community are frequency, numerical abundance, and areal coverage (Raunkiaer, '08; Smith, '13; Fuller and Bakke, '18; Nichols, '30; Romell, '30).

AREA STUDIED

The tract selected for investigation is a partly regenerated burn occupying 955 acres on the Arnot Forest in Schuyler County, southern New York. Its topography is fairly rough, with steep hillsides and V-shaped valleys. This broken character leads to a complexity of vegetation which is further emphasized by variations in altitude between 1,200 and 1,900 feet.

Severe fires following logging operations devastated a portion of the area in 1900 and the remainder in 1912. Some knowledge of early successional stages subsequent to the fires was obtained from the older local inhabitants, whose statements may be accepted that for a short time after each fire the burned area was largely barren. Then, along with a growth of hardy herbs, a dense stand of raspberries and blackberries sprang up, furnishing local people for a number of years with considerable quantities of fruit. Finally, after perhaps ten or twelve seasons, this growth gradually became choked out by the development of aspen, pin cherry, red maple, and other intolerant tree species which had started up under cover of the raspberry-blackberry community.

At present these intolerant tree species are still conspicuous in the upper canopy of the stand, although numerous individuals of climax species such as beech, sugar maple, black and yellow birches, basswood, ash, and hemlock may be found. As to the lower crown classes and reproduction—the portion of the stand which foreshadows its future composition—a detailed quantita-

tive analysis of the tract was necessary to give an accurate picture of their floristic composition.

As a result of this analysis, two distinct burn associations² were delimited according to the nature of their eventual climaxes. One of these was further subdivided into an association and two consociations showing distinctly different species compositions and degrees of development toward the climax. The subordinate association was finally divided into three site-quality phases on the basis of density of cover, vigor of tree growth, and soil moisture. Each community was given a name based on the dominant tree species occurring in the forest stand and a dominant of the herbaceous layer:

- | | | |
|---------------------------------------------------|---|--------------------------------------|
| I. <i>Fagus-Acer-Pteridium</i> phase | } | <i>Fagus-Acer-Betula</i> association |
| II. <i>Acer-Betula-Aster</i> phase | | |
| III. <i>Acer saccharum-Aster</i> phase | | |
| IV. <i>Carpinus-Acer-Waldsteinia</i> consociation | | |
| V. <i>Fagus-Solidago</i> consociation | | |
| VI. <i>Quercus-Populus-Pteridium</i> association | | |

The first five communities listed are various phases in the succession toward the northern hardwoods climax, and the sixth represents a development toward the *Pinus-Quercus-Castanea* climax.

METHOD OF ANALYSIS

A combination of the strip and quadrat methods was employed. The purpose of the two and one-half per cent strip survey was to obtain quantitative data on the species composition and size distribution of the larger tree-size classes in the various secondary communities, with the numerical distribution of the various species on an acre basis. Observations were also made of the environmental character of each community: of the slope and exposure of the area tallied, its soil character, depth, and moisture conditions, the density of woody and herbaceous ground cover, and the estimated abundance of tree reproduction. In the quadrat survey, based upon a thousand square-meter quadrats, a detailed picture was obtained of the lowest strata of vegetation, including tree reproduction and shrubs as well as all herbaceous species.

As a result of this study, the whole burned area was divided into the six communities discussed above and in the following statement of results, and described in table I.

The progress of succession of each community and the probable nature of its climax were determined from a study of the numbers of various tree species in each size class, and to some extent also from the relative abundance of herbs of mesophytic character.

Indicator plants were found for each community: species which are char-

² The ecological terminology proposed by Nichols ('30) is employed.

TABLE I. Summary of characteristics of secondary forest communities, Arnot Forest

Characteristics:	Community					
	<i>Fagus-Acer-Pteridium</i>	<i>Acer-Betula-Aster</i>	<i>Acer saccharum-Aster</i>	<i>Carpinus-Acer-Waldsteinia</i>	<i>Fagus-Solidago</i>	<i>Quercus-Populus-Pteridium</i>
Area, acres.....	397	198	57	5	2	296
Present dominant trees	<i>Fagus grandifolia</i> ; <i>Acer rubrum</i> ; <i>Populus grandidentata</i>	<i>Acer saccharum</i> ; <i>Acer rubrum</i> ; <i>Betula lenta</i>	<i>Acer saccharum</i> ; <i>Betula lenta</i> ; <i>Fagus grandifolia</i>	<i>Carpinus caroliniana</i> ; <i>Acer saccharum</i> ; <i>Populus tremuloides</i>	<i>Fagus grandifolia</i>	<i>Acer rubrum</i> ; <i>Quercus montana</i>
Future dominant trees	<i>Fagus grandifolia</i> ; <i>Acer saccharum</i> ; <i>Betula lenta</i>	<i>Acer saccharum</i> ; <i>Betula lenta</i> ; <i>Fraxinus americana</i>	<i>Acer saccharum</i> ; <i>Fagus grandifolia</i> ; <i>Betula lenta</i>	<i>Carpinus caroliniana</i> ; <i>Acer saccharum</i>	<i>Fagus grandifolia</i> ; <i>Acer rubrum</i>	<i>Acer rubrum</i> ; <i>Quercus montana</i>
No. trees per acre. . . .	9800	13400	15400	10800	11600	6300
Climax tree species, %	61	62	78	32	69	25
Area under sparse cover (plantable), %	15	13	3	25	0	40
Present dominant shrubs.....	<i>Diervilla lonicera</i> ; <i>Viburnum acerifolium</i>	<i>Diervilla lonicera</i> ; <i>Rhus typhina</i>	<i>Diervilla lonicera</i> ; <i>Hamamelis virginiana</i>	<i>Hamamelis virginiana</i> ; <i>Diervilla lonicera</i>	<i>Diervilla lonicera</i>	<i>Diervilla lonicera</i> ; <i>Kalmia latifolia</i>
Area occupied by shrubs, %.....	8	6	7	9	1	24
Present dominant herbs	<i>Pteridium latissimum</i> ; <i>Mitchella repens</i>	<i>Aster divaricatus</i> ; <i>Solidago arguta</i>	<i>Aster divaricatus</i> ; <i>Dennstaedtia punctiloba</i>	<i>Waldsteinia fragarioides</i> ; <i>Fragaria virginiana</i>	<i>Solidago arguta</i> ; <i>Solidago bicolor</i>	<i>Pteridium latissimum</i> ; <i>Gaultheria procumbens</i>
Area occupied by herbs, %.....	35	32	63	61	8	46

TABLE I. Summary of characteristics of secondary forest communities, Arnot Forest (Continued)

Characteristics:	Community					
	<i>Fagus-Acer-Pteridium</i>	<i>Acer-Betula-Aster</i>	<i>Acer saccharum-Aster</i>	<i>Carpinus-Acer-Waldsternia</i>	<i>Fagus-Solidago</i>	<i>Quercus-Populus-Pteridium</i>
Plant species:	26	23	21	16	5	28
Trees.....	23	18	14	4	2	19
Shrubs.....	70	69	48	39	12	64
Herbs.....	119	110	83	59	19	111
Environmental character:						
Aspect of the community.....	SW, S, SE, NE	E, NE, SE	N, NW, NE	South	SE	S, SE, SW
Average slope, %.....	12	10	20	2	20	22
Maximum slope, %.....	20	20	40	5	20	45
Minimum slope, %.....	0	0	0	0	20	5
Soil quality.....	Gravelly to rocky	Gravelly	Gravelly	Sandy	Gravelly	Rocky
Soil depth.....	Shallow	Medium	Medium	Medium to deep	Medium	Shallow
Soil moisture during growing season.....	Dry	Fresh to dry	Fresh	Fresh	Fresh	Dry
Remarks:	Tree growth generally scrubby, especially on ridges	Tree heights good	Tree heights and form excellent	Not a burn community; an old-field invasion	A pure beech-sprout phase of an old-field invasion	Species composition poor; tree form bushy and short

acteristic of their own burn community and of no other. However, it was demonstrated that the few plants which fulfilled these requirements invariably have such small frequencies and area percentage that their value as site or type indicators is low. For this reason, in naming the various communities, the names of the one or two dominant tree species and of the most conspicuous herb were used; this combination was considered more descriptive of a community from a forester's viewpoint than the name of a truly "characteristic" plant.

Indicators of another sort were discovered, however: plants which, by their abundance or scarcity in a community, are of value in indicating the community's progress toward its mesophytic climax. These are named and commented upon in the statement of results.

For a tentative determination of the feasibility of artificial introduction of commercial tree species to the burned area, an examination was made of several plantations of conifers and hardwoods which had been set out on different sites in the Arnot Forest in 1929, 1930, and 1931. Survival counts were made of all these plantations, and the results are tabulated in table II.

RESULTS

Succession on burned forest areas

1. The succession of the tract studied seems to resemble closely that other sections of the northern hardwoods region as described by earlier investigators (see above, under "Literature"). Accordingly the results of the present study may be considered applicable to secondary burn successions in the northern hardwoods in general.

2. Three of the six burn communities recognized are progressing in a satisfactory manner toward the beech-maple climatic climax. While their upper canopies are still characterized largely by the presence of intolerant trees such as aspen and pin cherry, sixty to eighty per cent of all the trees found in these communities are relatively desirable mesophytic climax species such as beech, black and yellow birches, hard maple, ash, basswood, hemlock, black cherry, red oak, yellow poplar, and white pine.

The *Carpinus-Acer-Waldsteinia* and *Fagus-Solidago* consociations also belong to the beech-maple succession, but show poor progress toward the climax and will require assistance through improvement cuttings and plantings.

The *Quercus-Populus-Pteridium* association is progressing very slowly toward a *Quercus-Pinus-Castanea* type, which is considered to represent in this region a physiographic climax occurring on warm south slopes. Its succession is undesirably slow, and should be aided by suitable planting.

3. The degree of development of any burn community toward its climax and the probable nature of the climax may be judged with a fair degree of accuracy by an analysis of tree species composition, especially in the smaller size classes, and by observation of the presence or absence of characteristically

TABLE II. *First-year survival of tree stock planted in three burn communities, Arnot Forest*

Species planted	Class ¹	Year planted	Per cent survival	Per cent vigorous
<i>Fagus-Acer-Pteridium Community</i>				
<i>Pinus resinosa</i>	2-1	1930	51	42
".....	2-1	1931	24	20
<i>Pinus strobus</i>	2-2	1930	64	60
".....	2-2	1931	90	85
<i>Picea glauca</i>	2-1	1930	63	59
<i>Picea abies</i>	2-1	1930	60	58
<i>Quercus borealis</i> , var. <i>maxima</i>	acorns	1930	83	83
<i>Fraxinus americana</i>	1-0	1930	73	73
<i>Acer-Betula-Aster Community</i>				
<i>Pinus resinosa</i>	2-1	1930	28	24
".....	2-1	1931	27	20
<i>Pinus strobus</i>	2-2	1930	36	31
".....	2-2	1931	86	70
<i>Picea glauca</i>	2-1	1930	38	31
<i>Picea abies</i>	2-1	1930	25	22
<i>Quercus borealis</i> , var. <i>maxima</i>	acorns	1930	61	61
<i>Fraxinus americana</i>	1-0	1930	69	66
<i>Quercus-Populus Pteridium Community</i>				
<i>Pinus resinosa</i>	2-1	1930	83	79
".....	2-1	1931	61	37
<i>Pinus strobus</i>	2-2	1930	77	73
".....	2-2	1931	98	91
<i>Picea glauca</i>	2-1	1930	86	84
<i>Picea abies</i>	2-1	1930	78	75
<i>Quercus borealis</i> , var. <i>maxima</i>	acorns	1930	91	90
<i>Fraxinus americana</i>	1-0	1930	91	86

¹ The heading "Class" indicates the planting age of the trees used: e.g. "2-1" describes trees grown two years in a seed-bed and one year in a transplant bed before field planting.

mesophytic herbs, such as *Aralia nudicaulis*,³ *Arisaema triphyllum*, *Clintonia borealis*, *Dentaria diphylla*, *Hepatica acutiloba*, *Medeola virginiana*, *Polygonatum biflorum*, and *Tiarella cordifolia*.

4. The individual forest communities described in this study may best be recognized by a combination of the following criteria: (a) the sites on which they occur; (b) the dominant tree species on the basis of total numbers; and (c) the most conspicuous plants in the herbaceous layer (see table I). This combination of features is considered a more reliable indicator than any single characteristic plant.

5. Sites suitable for planting may be recognized by their open cover and the presence in some abundance of herbs such as *Apocynum androsaemifolium*,

³ Nomenclature is according to Gray's "New Manual of Botany."

Aster prenanthoides, *Epilobium angustifolium*, *Fragaria virginiana*, *Gaultheria procumbens*, *Pteridium latiusculum*, and *Waldsteinia fragarioides*.

Silvicultural Treatment of the Communities

Several possible modes of treatment might conceivably be applied to any forest burn community in order to hasten or alter its development:

1. Complete conversion to conifers might be attempted. In the writer's opinion this method is not at all to be recommended, because of the high cost of establishment of such stands and of their maintenance against the encroachment of the natural forest, their susceptibility to epidemic attack by insects and disease, and their asserted tendency to impoverish the soil.

2. Conifers such as red (Norway) or white pine might be introduced by planting, with the purpose of producing eventually a mixed pine-hardwoods forest, the planted stock being scattered in favorable places through the existing hardwood stand.

A portion of each of the communities described, scattered in patches through the burned area, is characterized by thin tree cover and correspondingly low shade and root competition, as well as by the presence of relatively xerophytic herbs and shrubs (as listed under "5," p. 289). In these places, planting of coniferous species such as red or white pine would very likely result in their successful establishment. The use of large transplants such as four-year (2-2) stock is advised for this purpose, because of the apparent low availability of soil moisture and probable severe competition by the abundant ground cover.

The ultimate result of this planting would be a mixed stand of hardwoods and pine. It is felt that conversion to such a stand is to be recommended wherever possible, because of its superior economic value and since existing stands of this sort seem to a high degree to be in harmony with their environment.

3. Whether or not conifers are introduced, the species composition of the stand should be improved by cleanings, or by later improvement cuttings or thinnings, for the purpose of favoring the better species or individuals.

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REVIEWS

ON THE DYNAMICS OF VERTEBRATE POPULATIONS¹

This is an important contribution (in English) by a Russian worker on populations. He is to be commended for the splendid job he has done in spite of his lack of contact with other workers in the field.

The first part is given over to a very interesting and valuable discussion of the theoretical mathematics of populations. Page 412 contains a graph of theoretical curves of population increase, with a mathematical discussion similar to theoretical increases given by Leopold (*Game Management*, 1933) and others. The theoretical population increase agreed with the actual in the early stages of increase, but as usual, the theoretical breaks down after the first few years.

The author finds that this theoretical rate of increase follows the exponential curve determined by the constants of reproduction and juvenile mortality.

The second part of his treatise contains statistics on grouse and the roe deer from the former imperial shooting preserve at Gotchino, near Leningrad, from 1886 to 1909. Unfortunately, details of the population—the exact area covered, age of young at registration (census)—are not given.

Page 419 contains a table showing breeding population and the number of young produced in the summer. The percentage shot is also given, but he does not state if it is the percentage of the total population or of the young only. Severtzoff also determines the *winter survival* of young on the basis of the *increase in breeding population the following summer*. This is not a legitimate assumption. The breeding population indicates the winter survival of the *total population*, both young and old.

Page 422 contains a graph of the roe deer on this area resulting from introduction in 1892 of 20 bucks and 21 does. The hunting factor was negligible and the subsequent additional introduction was also slight. It is interesting that the curve of increase resulting is substantially the same as the Pennsylvania curves from similar introductions.

The census method is not fully explained, but it is mentioned that deer "... were registered by tracks left by them in the snow." The author should have gone into considerable detail on this census method, which may work in Russia, but has not worked successfully in America.

The author considers that short plagues can be caused only by abiotic factors (*e.g.*, weather, starvation, etc.), while the long plagues can be caused

¹ Severtzoff, S. A. (Laboratory of Evolutionary Morphology of the Academy of Science of U. S. S. R.) 1934. On the dynamics of populations of vertebrates. *Quarterly Rev. Biol.* 9 (4): 409-437.

only by biotic factors (*e.g.*, disease). This seems a most illogical conclusion. Weather cycles, for example, may progressively grow favorable or unfavorable, and take many years to do it. Increased food supply may be progressive, etc.

Severtzoff discusses Volterra's hypothesis and the relation of his own work to Volterra's findings, and decides that predators may be the cause of the grouse declines. This assumption (if he means predators in the American sense) runs counter to the work of Americans, who reveal that predation is not the universal answer.

The mortality of the young is set at 90-95 per cent in birds and at 50 per cent in mammals. (This blanket statement by the author is too general and we most seriously reject it.) In birds "... the fluctuation in the mortality rate probably depend on the changes in the numbers of the predators. The curves showing the shooting off of the predators correspond to the curves in the numbers of the game." The reviewer believes that a different interpretation of the curves fits better. It would seem more logical that the increase in numbers of predators shot indicates an increase in population parallel with the game population. This correlative increase occurs more often than supposed and may be the universal rule if we think in terms of generalized prey (*i.e.*, primary prey, buffer species, etc.). American work has shown that game cycles usually run in phase with the predators and not opposite, as would be the case were predators the lethal agent. It is of interest that the author expresses this view farther on, saying: "The curve representing the dynamics of the carnivorous species preying upon the herbivorous ones runs parallel to that of the herbivorous species. . . ." The author evidences an unfamiliarity with the recent work of Paul L. Errington, which shows that in some species, at least, predation acts only upon the vulnerable surplus above the carrying capacity of the environment. Dr. Errington's Law of Vulnerability is the most important single contribution to the understanding of predation. Any future investigation of predation will not be complete unless carrying capacity and consequent vulnerability are considered.

A casual observation by the author that "the depressions take a more rapid course when they affect more fertile species and a slower course when affecting less fertile ones," is very interesting and, if true, a contribution of importance to the field of cycle research.

The author assumes "the duration of life of the individuals to correspond to the frequency of the plagues." We know very little about the life span of animals, but recent cycle studies by the reviewer do not corroborate this assumption.

The paper under review might better have been published in a journal of natural history or ecology, where the editor would have helped the author over the hurdles of American nomenclature. As it is, a confusion of terminology will cause unnecessary misunderstanding among students of wild life and ecology which could have been avoided by a competent editor.

It seems advisable for the reviewer to supply a wild-life interpretation to some of the author's terminology. In many cases the author uses one word for several different connotations not necessarily synonymous.

<i>Author's Terminology</i>	<i>Wild-life Terminology</i>
register	census, count, tally
plague	cycle, die-off, decline, low, population drop, mortality, epizootic
predators	disease (parasitic, bacterial, virus), predators (<i>sic</i>), enemies
herd	population, adult population, covey, flock, herd (<i>sic</i>)
brood	total young, chicks, fawns
increase and decline	cycle, irruption
depression	cycle low, population low
fertility	reproductive rate, population increase, reproductive potential, breeding potential, reproductive efficiency, fecundity

LEONARD WILLIAM WING

UNIVERSITY OF WISCONSIN,
MADISON, WISCONSIN

THE MIGRATION OF ANIMALS FROM SEA TO LAND¹

Professor Pearse's monograph is another bit of evidence that American biologists are actively interested in consolidating advances as well as in undertaking new, pioneering explorations. Formerly this sort of writing was left largely to European, particularly to German scholars. The present work starts with the origin of life in the sea and evaluates the routes taken from sea to land, discusses causes of the migration and the changes in animal structures and physiology as the migration proceeded and closes with a brief summary of what land animals have attained. The point of view is that of physiological rather than physiographic ecology.

The work is frankly a compilation in the modern style with much direct quotation and with careful citation of sources. The bibliography covers pages 131 to 174 inclusive; it lists recent literature mainly and almost without exception stops short of 1935. The text is unusually free from factual errors. The only one that has caught my attention is the statement (p. 49) that "the amount of oxygen in the ocean is quite constant at all depths." For a conflicting report see Schmidt (*Science*, 61: 592).

The Duke University Press is to be commended for their enterprise in publishing this valuable source book.

W. C. ALLEE

THE UNIVERSITY OF CHICAGO

¹ Pearse, A. S. 1936. The migrations of animals from sea to land. *Duke University Press, Durham, N. C.* x + 176 pp. \$3.00.

A BACKGROUND FOR STUDIES IN BEHAVIOR¹

The present volume is the first of a series of three by these authors in which they plan to cover the field of plant and animal behavior from the point of view of comparative psychology. The remaining volumes will consider respectively the behavior of plants and invertebrates (Vol. II) and of vertebrates (Vol. III). The authors announce that in the present volume they intend "to provide the student with the proper background for an understanding of the survey of plant and animal behavior to be covered in the two later volumes. The first four chapters (pp. 3-166) offer a broad historical and theoretical approach to the viewpoint and problems of comparative psychology. The next two chapters represent a pioneer attempt to systematize the methodology of the science. The final chapter (pp. 273-397) comprises a comparative study of the receptive, transmissive and reactive mechanisms of living organisms." A bibliography of 68 pages and excellent indexes complete this volume. The book is adequately illustrated.

The careful student will need to supplement the historical account by reading that given in S. J. Holmes' *Studies in Animal Behavior* with particular reference to the earlier periods. There is, however, nothing in print known to me which so completely and fairly appraises the historical combined with the general biological background of behavior. The point of view is always that of the comparative psychologist and perhaps for this reason the authors have undertaken to review carefully certain aspects of the psychological background usually hastily covered by biologists who write on animal behavior. And since the book is apparently written primarily for the psychological audience, they have similarly reviewed aspects of the biological foundations of behavior all too frequently taken for granted by biologists.

The philosophical approach also is adequate; for example, I know of no similar summary of the present status of the vitalism-mechanism situation in language which the intelligent undergraduate can appreciate. The approach to all these problems is pleasantly objective and is consistently divorced from the anthropocentric point of view of human psychology; that is, the authors move steadily toward setting up a comparative study although more attention is given to the vertebrates than their numbers deserve.

True to their objectivity, the authors examine and reject certain modern tendencies toward teleology and vitalism and attempt to show (p. 56) "that the facts of regulation in living systems can be adequately dealt with in terms of physico-chemical theory, provided the latter is restated along organismal lines, without recourse to teleology or vitalism." Organicism is correctly regarded as applying, in part, at least, to non-living as well as to living systems and mechanistic theory is rightly identified as being "nothing more than another name for scientific determinism." Used in this connection there is

¹ **Warden, C. J., T. N. Jenkins, and L. H. Warner.** 1935. Comparative psychology. Vol. I. Principles and methods. New York, The Ronald Press Co., 506 pp. \$4.50.

no objection to the emphasis placed on the doctrine of emergence and the reader is warned (p. 79) against certain tendencies which would expand this doctrine into a metaphysical theory.

Relatively little use is made of the all too frequent emphasis in writings on emergent evolution that the whole is something more than the sum of the parts and the often cited case of properties of water not being predictable from existing knowledge of the properties of hydrogen and oxygen is stated in its historical setting only. In fact this argument is, on the one hand, merely chiding chemists for not yet having gained their goal of being able to do exactly this sort of predicting and on the other hand is but a half truth since, in the present state of knowledge, given the properties of water, one could not predict without *a priori* knowledge of its chemical constitution, the properties of its constituents. Turning the well worn words about, we see here that the sum of the parts may be greater than the whole. This is, however, a personal digression.

Ecologists will be interested in the basic position given to interrelations between organisms and their environment. Spencer's remark that "life itself is constituted by the continuous adjustment of internal and external relations" is quoted with approval (p. 82), while the term "organism" is explained to carry always the implication of the more exact statement of "organism-in-environment." As such, the whole field of behavior is seen to exist, as some have recognized for years, as an integral phase of ecology. Comparative psychology is closely related to physiology; while the physiologist limits himself very largely to a study of internal factors and to the simpler interrelations between organisms and environment, the comparative psychologist places emphasis upon the larger interrelations of the latter type and must seek their explanation, at least in part, in the investigations of the physiologist.

Due weight is given to the importance of the phylogenetic approach to the study of the behavior of species, and the chart given on page 278 emphasizes the specialization of modern representatives of the Protista as well as of modern chordates or arthropods. This chart indicates that the echinoderms and chordates are more closely related to each other than to other phyla, and thus recognizes the validity of certain aspects of the "diphyletic tree." This is at variance with the chart given on p. 101 in which there is no hint even of the well established close relationship between annelids and mollusks.

Throughout, the authors give evidence of close and intelligent attention not only to the work of people interested in animal behavior proper such as Jennings, Loeb, Mast and Verworn, but also to that of general biologists such as Child, Lillie, Henderson and Wheeler and to that of ecologists, especially to Shelford's summarizing book on methods. The use of these materials is essentially sound; it is the more to be regretted, therefore, that they have chosen to rely on Parker and Haswell's textbook as their guide in classification; excellent as this classic is in many phases of zoology, it is not good in taxonomy.

Almost all behavior is regarded as a resultant of hereditary and of environmental forces. There are no known criteria for behavior that is predominantly determined by the environment; behavior mainly determined by heredity is usually considered to be that which is shown after birth without the benefit of previous obvious experience. Because of the difficulties inherent in this situation, the distinction between innate and conditioned behavior is discarded as one of the major means of classification of the subject. There-with a whole series of terms is dropped, *e.g.*, reflexes, tropisms and instincts. What have been generally known as tropisms are now to be called *orienting responses* or *growth responses* as the case may be. *Response* or *reaction* rather than *reflex* is considered to be the unit of behavioral analysis and perhaps in the following volume a clear, unequivocal definition of this unitary response or reaction will be given. *Instinct* is to disappear and *habit* is to be substituted for all such acts in which the environment plays a significant rôle. No name is proposed for the "small class of more rudimentary behavior patterns generally recognized as dominantly hereditary."

The general classification of behavior which is proposed may be outlined as follows:

I. RECEPTIVE CAPACITIES

<i>Capacity</i>	<i>Stimulus Domain</i>
Chemoreception	Chemical
Photoreception, etc.	Light, etc.

II. REACTIVE CAPACITIES

Action systems; feeding behavior; protective behavior; reproductive behavior; special types of behavior, orientation, *e.g.*; motivation; modifiability; general intelligence.

All known systems of classification of behavior, including that proposed in this book, are faulty and inconsistent. It is unfortunate from my point of view that if reflexes, tropisms and instincts are to be thrown overboard, that the equally misused term *habit* did not follow. It will be interesting to watch the review of behavior with this classification through the next two volumes. We shall then be in a better position to judge the system on its merits.

The drastic attitude taken regarding hereditary patterns of behavior makes it all the more important that interested students should undertake to determine how much of different behavior patterns is really innate as shown by the application of modern genetic techniques and how much is in fact environmentally determined.

Space does not permit discussion of the "action-tendency" concept which occupies an important position in the organization of the book, nor of other interesting subjects such as the relation between behavior and speciation. The chapters on methods will be helpful for beginning experimentalists and

the long discussion on comparative morphology and physiology is as useful for students of general zoology as for those interested primarily in comparative psychology.

To a much greater degree than usual, I find myself seriously impressed by the accuracy, skill and good judgment used in the selection and presentation of this material.

W. C. ALLEE

THE UNIVERSITY OF CHICAGO

VERNALIZATION

Probably no scientist has done more than Klebs to upset the concept that the cycle of plant development is altogether constant and conditioned only by internal hereditary characters. He has presented the results of many experiments which show that the reproduction of plants, as well as other life processes, are to a great extent subject to the external environment and that man by modifying this environment may often change the order and extent of these processes.¹ In his last study he recognized three distinct stages in the flowering of *Sempervivum* controlled by definite sets of modifiable external conditions.²

A practical application of similar principles has recently been attempted in an effort to hasten the development of certain economic plants and more particularly to change the habits of crop production by transforming winter cereals into annual plants producing a crop the same season in which they are sown. This transformation has received most attention in the Soviet Union and the results of extensive experiments have been published almost exclusively in the Russian language.

It is, therefore, important that Maximov, a distinguished Russian plant physiologist, has discussed in English these transformations, known as "vernalization."³ He points out that Lysenko of the Odessa Institute of Plant Breeding has been the leading investigator and has elaborated a method of subjecting slowly germinating seeds of winter wheat to a temperature little above 0° C. for periods of 10 to 60 days. This "vernalized" winter wheat is sown and treated like spring wheat and it heads and produces a crop the same season.

Upon this and similar experiments Lysenko has based hypotheses of decided importance to ecologists and plant physiologists. His theoretical concepts are that growth and development are not identical phenomena; that the entire process of the development of an annual seed plant consists of individual steps or stages which are always in a strict sequence and a subsequent

¹ Klebs, G. 1913. Physiologie der Fortpflanzung. *Handwörterb. Naturw.* 4: 276-296.

² ——. 1918. Ueber die Blütenbildung von *Sempervivum*. *Flora* 111-112: 128-151.

³ Maximov, N. A. 1934. The theoretical significance of vernalization. *Imp. Bur. Plant Genetics, Herb. Publ. Sc. Bull.* 16.

stage can not set in until the preceding stage has been completed; and that different stages of development of the same plant require for their completion different external conditions.

These concepts are carefully discussed by Maximov who considers them well founded but probably subject to modification by the results of further experimentation.

In a more recent publication,⁴ Lysenko's theories are brought to us in more detail and some of the stages of development which he recognizes are differentiated. The first of these is the "vernalization" or "thermo-stage" which for plants like winter wheat is characterized by prolonged low temperature. This must be completed before the initials for the reproductive organs can be laid down. The temperature range and the time of exposure differs for different varieties and for different species. The method of vernalization thus aims at providing the plant with the necessary conditions for the completion of this first stage before the seeds are sown.

For many plants, including wheat, the second stage includes conditions of light and may be known as the "photo-stage." The discussion of this stage makes it evident that a different interpretation of light effects may be found necessary for "short-day plants."

A third stage, still imperfectly understood, seems to follow the photo-stage and seems associated with gametogenesis.

In addition to the results of Lysenko's investigations, many now appearing for the first time in English, the results obtained by many other Russian workers are given in considerable detail. These serve to indicate how extensively vernalization has been investigated within the Soviet Union.

Investigations in many other countries including the United States and Canada are also summarized in this useful bulletin which makes available in English the results of many workers many of which were published in various other languages. Almost a hundred citations are included in the bibliography. The various investigations give results which support Lysenko's theories to a varying extent but sufficiently to prove that vernalization is worthy of the careful attention of all plant scientists.

GEO. D. FULLER

THE UNIVERSITY OF CHICAGO

A COMPILATION ON FERNS¹

This book would seem to require attention here because in reviews of it which have appeared in other journals there has been a suggestion that it has some ecological bearing or basis. Actually, the lack of trustworthy ecological data in its pages is little short of amazing. The book seems to have been com-

⁴ **Imperial Bureaux of Plant Genetics.** 1935. Vernalization and phasic development of plants. *Imp. Bur. Plant Genetics. Bull.* 17.

¹ **Roberts, Edith A., and Julia R. Lawrence.** 1935. American Ferns. How to Know, Grow, and Use Them. *Macmillan.* 98 pp. \$2.50.

piled from manuals and writings by amateurs, and is replete with technical errors and misunderstandings. The results of growing spores in culture solutions are presented, but this is so artificial that abnormal plants often result, as evidenced by the cuts labelled *Aspidium cristatum*, *A. marginale*, and *Asplenium ruta-muraria*, the last looking like the result of a wilting-coefficient experiment.

The term association is much used, but in a largely theoretical if not imaginary sense. Species which do not and can not grow together in nature are repeatedly placed in the same "association." Swamp-plants and dry rock-plants, sun and shade plants, pioneer and climax plants are mixed together in tabulations and planting-plans. Not a word is included as to the preference of certain species for acid, neutral, or alkaline soils, and the one time limestone application is mentioned is in connection with the walking fern, which does not need it. Phenological data given are untrustworthy.

From the conservation standpoint the book is unfortunate because rare species which need protection are recommended for cultivation in situations where they will promptly die. The harts-tongue is erroneously stated to occur in an "oak association" and to be easy to grow. The climbing fern, widely recognized as a plant of the most acid bogs, is recommended for cultivation beside the wall-rue, a plant of dry limestone cliffs. From the ecologist's standpoint the publication of such a book is regrettable.

EDGAR T. WHERRY

UNIVERSITY OF PENNSYLVANIA,
PHILADELPHIA, PA.

POLLEN GRAINS¹

In view of the increasing interest in the occurrence of pollen in the earth and in the air a monograph on pollen grains is most timely. While the study of the morphology of pollen dates to the early use of the microscope no exhaustive study has appeared in English and few foreign publications are of recent date as will be evident from an examination of the historical review presented by Wodehouse.

The major portion of the present volume is devoted to a description of the pollen of various genera and species together with keys and a system of pollen classification. The descriptions are elaborate and are clarified by excellent and numerous illustrations. The author is convinced that the pollen patterns may prove of service in elucidating genetic relationships, especially in certain groups of the Compositae.

The occurrence of atmospheric pollen and its effects in producing hay-fever is discussed in two chapters. It is evident that the book will be of service to physicians who are engaged in the study and treatment of hayfever and similar diseases.

¹ **Wodehouse, R. P.** 1935. Pollen grains: Their structure, identification and significance in science and medicine. x + 574 pp. 14 pl. 117 fig. McGraw-Hill Book Co., New York. \$6.00.

The usefulness of tree pollens, preserved in peat deposits, in interpreting the vegetation and climates of past ages is now well recognized. The chapter on pollen statistics, and the methods employed in their development, has been contributed by Dr. G. Erdtman, the leading Swedish expert in the technique of these methods of botanical and geological research.

The reviewer is not, however, favorably impressed with the teleological philosophy of the author. The discussion of plants "combatting" and "encouraging" the visits of insects is certainly not in accord with the attitude of modern scientists. It seems strange that plants have "tried the experiment of entomophily," have "abandoned" insect pollination, and have "returned" to pollination by the wind. One wonders what "experiment" they have now in progress.

The entire volume, however, shows evidence of careful investigation, there is an abundance of detail which seems to be accurate, and the printers and publishers have done their work well. The results are a volume that is sure to be useful although in somewhat limited fields.

GEO. D. FULLER

THE UNIVERSITY OF CHICAGO

ARCTIC BUTTERFLIES ¹

No temperatures that are found in nature are too low for butterflies. In the most northerly lands on earth, Grinnell Land and Grant Land, above 82° in latitude, live five species of butterflies as well as two kinds of bumble bees. During the short month when the sun never sets butterflies are continually on the wing. The caterpillars feed over a slightly longer period, but all the active life of the insects is compressed within six weeks. During the winter the caterpillars are frozen as hard and as brittle as icicles but begin to feed again when it warms up.

But there are large regions further south in lower arctic countries in which there are no native butterflies: Spitzbergen with Bear Island, Franz Josef Land, Iceland, and even the Aleutian Islands where the minimum temperature is 7° F. and the soil does not freeze more than a foot in depth and in some winters not at all.

In the Antarctic one butterfly occurs on the Falkland Islands and about a dozen, the majority of which closely resemble arctic types, on the southern tip of South America, but none on the Antarctic continent or the islands of the south polar sea, though on Kerguelen the winter temperature seldom goes below 32° F. It is thus clear that while butterflies are indifferent to temperature, they require sunlight and do not thrive in wet, cloudy countries.

In geographical distribution and in many of their ecological relations arctic butterflies are like arctic plants. Thus most of the arctic butterflies range

¹ Clark, Austin H. 1935. Arctic butterflies. *Smithsonian Annual Report for 1934*, pp. 267-296.

widely all around the pole and extend far southward into temperate latitudes. "The butterflies of the far north and those of alpine regions are very variable from place to place and run into many puzzling forms," and it becomes a difficult matter to decide whether they are best dealt with as a few large polymorphic species or as many local species. Like arctic plants, they are a mixture of species which are strictly alpine in their southern extensions, with others which in the south are common lowland forms. "For instance, the little Copper (*Chrysophanus phlaeus*) is not an upland species in Africa or in Japan, nor is it a true upland butterfly in the southern portion of the United States. The grizzled skipper (*Pyrgus centaureae*) becomes an alpine butterfly in our western mountains and in Asia in the Altai; but it is a lowland butterfly from southern New York southward to Virginia."

Like the plants, the butterflies of the far north have few structural peculiarities but are of smaller size than in the south. It is interesting to observe that the early spring individuals captured in the south may closely resemble the arctic forms, while the later summer forms are markedly different. Likewise where the southern butterflies have different forms in humid and arid country, the arctic types resemble the "dry form." They thus fit the plant ecologist's concept that the physiological effect of cold is the same as of drouth.

ROBERT F. GRIGGS

THE GEORGE WASHINGTON UNIVERSITY

TERMITES¹

Termites are found in every state in the union and are of importance in many ecological communities. Their excavation of soil, their rôle in the disintegration of wood and grass, their relations with fungi, their place in the food chain of many animals, their complex relationships with termitophiles and parasites, and their symbiotic relations with protozoa have made them objects of study by many ecologists. Their intricate social life, adaptive adjustment and coordination may also well be considered a phase of ecology. The evolution of this social life offers fine material for a study of certain phases of the evolutionary mechanism. The demonstrated specific variation in nest building behavior, clearly inherited and yet exhibited in its most elaborate form only by the sterile castes, is one of the best controlled examples of non-Lamarckian evolution.

Dr. Snyder has been known for years as the most outstanding American authority on termites. He is not only the best student of the economic control of termite damage, but has added fine studies of termite biology, morphology, distribution, ecology and taxonomy to the literature. His new book is a condensation, written in popular language, of his years of intimate

¹ **Snyder, T. E.** 1935. Our enemy the termite. *Comstock. Pub. Co., Ithaca, N. Y.* \$3.00. xii + 196 pp. 56 figs.

acquaintance with these insects. Half of the book is devoted to the economic phases of the subject, but the chapters on nests, food, guests, balance of nature, as well as the chapters on social organization and activity will interest the ecologist. The book is amply illustrated, contains a glossary and is well indexed. It should be in every reference library and in the hands of every investigator dealing with a termite problem.

ALFRED E. EMERSON

THE UNIVERSITY OF CHICAGO

MAYFLIES ¹

All students of limnology will welcome the comprehensive treatise on mayflies prepared by Needham, Traver, and Hsu. About 500 pages are devoted to a taxonomic monograph of North American mayflies with descriptions, keys, and figures of the adults and nymphs. A series of chapters deal with the external and internal anatomy. The chapters of special interest to the ecologist are those dealing with the life history, adaptations, and causes of mortality. This book will doubtless be the standard work on this order of insects for many years to come.

ALFRED E. EMERSON

THE UNIVERSITY OF CHICAGO

INSECTS OF SHADE-TREES ¹

Although this book deals with insects attacking trees commonly planted near the habitations of man, so many of the hosts are also wild trees in this country that many ecologists will find this work valuable in dealing with the interrelationships of insects and trees. The arrangement of the subject matter is according to the host trees and each chapter is amply illustrated with figures illustrating the damage and the insect species involved. The bulk of the text deals with the descriptions, life histories, and methods of controlling each important insect pest. The book will doubtless be a standard reference work in this field.

ALFRED E. EMERSON

THE UNIVERSITY OF CHICAGO

¹ Needham, J. G., J. R. Traver and Y. Hsu. 1935. The biology of mayflies. *Comstock Pub. Co., Ithaca, N. Y.* xiv + 759 pp. 40 pls. \$7.50.

¹ Herrick, G. W. 1935. Insect enemies of shade-trees. *Comstock Pub. Co., Ithaca, N. Y.* viii + 417 pp. 321 figs. \$5.00.

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PROCEEDINGS

BUSINESS MEETINGS OF THE ECOLOGICAL SOCIETY OF AMERICA AT ST. LOUIS, MISSOURI, DECEMBER 31, 1935, AND JANUARY 1 AND 2, 1936

Meeting of December 31, 1935

The Society met at Washington University at 9:45 A.M., President Taylor presiding.

The President announced the appointment of the following committees: Resolutions Committee: Francis Ramaley (chairman), C. T. Vorhies. Auditing Committee: L. M. Turner (chairman), S. A. Cain. Nominating Committee: George D. Fuller (chairman), G. E. Nichols, W. C. Allee. Publications Committee: A. G. Vestal (chairman), E. Lucy Braun, W. C. Allee.

A resolution offered by V. E. Shelford from the Committee on the Preservation of Natural Conditions was referred to the Resolutions Committee.

Dr. E. Lucy Braun's proposal of a plan for establishing National Primeval Monuments, principally as means of preserving for all time some of the few remaining areas of primeval vegetation, was unanimously endorsed by the Society.

The Society approved unanimously the proposal that the Lynn Fork of Leatherwood Forest, Kentucky, be made the first National Primeval Monument.

The Society voted unanimous approval of the aims and activities of the Save-Kentucky's-Primeval-Forest League. President Taylor appointed Dr. G. E. Nichols to be the Society's representative on the League's Advisory Council.

The meeting adjourned at 10:10 A.M.

Business Meeting of January 2, 1936

Following the papers presented Thursday morning, in Eads Hall, Washington University, President Taylor opened the second business session at 11:15 A.M. Reports of officers and committees were first called for.

REPORT OF THE SECRETARY-TREASURER

December 1, 1934 to November 30, 1935

RECEIPTS AND DISBURSEMENTS

Receipts

Cash on hand, as in report for preceding year	\$ 585.24
Dues from members	2,001.27

Interest	16.91
Royalty, Naturalists' Guide	8.00
Contributions (received by Treasurer)	5.00

Total receipts	\$2,616.42
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Disbursements

Ecology, payments for members	\$1,501.50
Ecological Monographs, payments for members	410.00
Printing, Bulletin (Dec. 1934 to Oct. 1935 nos.)	183.56
Other printing	41.54
Addressograph plates and work	2.50
Clerical work	51.34
Preservation committee	10.63
Nomenclature committee	12.00
Postage	59.80
Express and telegrams	13.04
Secretary's expense, Pittsburgh meeting	35.30
Copy of articles of incorporation	2.25
Bank charges, exchange	1.27
Supplies60
Refund of dues	10.00

Total disbursements	\$2,335.33
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Balance on hand	281.09
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\$2,616.42

ASSETS AND LIABILITIES AS OF NOVEMBER 30, 1935

Assets

Cash on hand	\$ 281.09
Accounts receivable, interest	16.00
Bonds (face value \$900) estimated value	450.00

Total assets	\$ 747.09
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Liabilities: Bills payable

None	
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REPORT OF THE AUDITING COMMITTEE

We have examined the report of the Secretary-Treasurer and believe it to be a correct statement of the Society's financial transactions.

(Signed) LEWIS M. TURNER

STANLEY A. CAIN

The reports of the Secretary-Treasurer and of the Auditing Committee on motion duly seconded were accepted.

REPORT ON MEMBERSHIP, 1935

Additions to membership during 1935	106
Losses during 1935 (lapsed 35, deceased 4, resigned 5)	44
Net gain	62
Last year's net gain	5

Additions by year for which journal subscription begins:

As of Jan. 1, 1934; joined during 1933	4
As of Jan. 1, 1935; 24 joined during 1934, 53 during 1935	77
As of Jan. 1, 1936, joined during 1935 (includes 8 whose applications were received during St. Louis meeting)	49
	<hr/> 130

Membership on March 1, 1935 (ECOLOGY 16: 270)	537
Net increase since that time	87

Membership at close of St. Louis meeting	<hr/> 624
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Respectfully submitted,

A. G. VESTAL, *Secretary*

The report was accepted.

REPORT OF THE BUSINESS MANAGER OF ECOLOGY FOR THE FISCAL YEAR, DECEMBER 1, 1934–NOVEMBER 30, 1935

Receipts

Cash on hand (statement of 1934)	\$1,688.90
Dr. Arthur G. Vestal, treasurer, E.S.A.:	
500 ½ members at \$3.00	1,501.50
Subscriptions: 1935	\$1,577.55
1936	482.20
	<hr/> 2,059.75
Single numbers and back volumes	282.47
Authors' payments	9.33
Authors' excess pages	33.87
Contribution for July issue;	
Dedicated to Henry C. Cowles	778.39
Genetics subscription included in ECOLOGY check	5.75
Ecological Society Membership drawn to ECOLOGY	4.00
Postage for number sent by airplane38
	<hr/> \$6,364.34

Disbursements

Printing

Lancaster Press, Inc.	\$4,038.29
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Illustrating

Revere Photo Engraving Co.	607.52
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Advertising

.....	139.64
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Office Expenses

Business:

Clerical Assistant for 12 mos. at \$10.00	\$ 120.00
Stationery	7.61
Postage	97.00
Wrapping paper and twine	8.68
Express charges	3.57

Editorial:

George D. Fuller	70.80
Alfred E. Emerson	22.44
	<hr/> 330.10

Miscellaneous

Refunds on single numbers	\$	2.40	
Registration fee—A. A. S. exhibits		1.50	
Audit of books for last fiscal year		5.00	
Genetics subscription included in ECOLOGY check		5.75	
Ecological Society membership drawn to ECOLOGY ..		4.00	
Government tax on checks62	
Collection charges30	19.57

Balance, November 30, 1935	1,229.22	\$6,364.34
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Cash in Bank	\$1,077.57
Checks in hand	139.50
Items placed for collection ...	12.15
Balance	<u>\$1,229.22</u>

Examined and found correct, December 16, 1935.

H. P. SCHOENBERNER,
Auditor

ASSETS AND LIABILITIES

Assets

Cash in Bank	\$1,077.57	
Checks in hand	139.50	
Items placed for collection	12.15	\$1,229.22

Bills Receivable

Subscriptions: 1935	\$	4.38	
1936		52.35	56.73
Single numbers		2.50	
Prof. J. E. Weaver		98.79	\$1,387.24

*Liabilities**Bills Payable*

Revere Photo Engraving Co.	\$	19.03	
Assets over Liabilities		1,368.21	\$1,387.24

Circulation data as per mailing list of the October issue:

	1934	1935
1. Members	456	434
2. Subscribers	424	462
3. Exchanges	93	99
4. Advertisers	12	12
5. Editorial office	2	2
	<u>987</u>	<u>1,009</u>
Number of copies printed per month	1,175	1,200

(Signed) C. STUART GAGER,
Business Manager of Ecology

The report was accepted.

REPORT OF THE EDITORS OF ECOLOGICAL MONOGRAPHS

On behalf of Dr. R. O. Rivera, Executive Secretary, Duke University Press, and Business Manager of *Ecological Monographs*, we present the following report for *Ecological Monographs* for the fiscal year ending June 30, 1935:¹

<i>Income:</i>		<i>Expense:</i>	
Advertising	\$ 625.00	Advertising	\$ 386.00
Subscriptions	1,330.07	General Expense	10.06
		Printing	2,702.49
	<hr/>		<hr/>
	\$1,955.07		\$3,098.55
Deficit		\$1,143.48	

The circulation of this journal is as follows:

Paid subscriptions	181
Duke University Library exchanges	14
Free exchange and complimentary	27
	<hr/>
	222

(Signed) A. S. PEARSE,
C. F. KORSTIAN,
Joint Editors

REPORT OF THE EDITORS OF ECOLOGY

We have been able to publish 680 pages this year as compared with 456 pages last year. This increase is partially a natural increase because of the healthy state of the journal's finances, partially because of the contributions made for the publication of the July number, dedicated to Dr. Henry C. Cowles, and partially owing to payments for early publication and for extra pages.

We have no reason for suggesting a change in editorial policy or the standards of acceptance for papers which were briefly discussed in our report for the year 1934 (see *ECOLOGY* 16: 272). At the present time the journal has been able to publish most papers within the six months following their preparation for publication. In other words many papers which offer no editorial difficulties are being published promptly, but those which present necessities of alteration before final acceptance may be delayed for a longer or shorter time in proportion to the difficulties presented.

The editors wish to take this occasion to thank the members of the Editorial Board for their cooperation and also wish to express their appreciation

¹ As Duke University Press prints and publishes the *Ecological Monographs* it seems desirable that the annual reports of this journal should be for the fiscal year of Duke University.

to Dr. W. S. Cooper for his services in arranging the contributions and in the selection of the papers for the issue dedicated to Dr. Cowles.

(Signed) GEO. D. FULLER,
ALFRED EMERSON,
Joint Editors

The reports of the editors of ECOLOGICAL MONOGRAPHS, and of ECOLOGY were accepted.

REPORT OF THE COMMITTEE IN CHARGE OF THE COWLES NUMBER OF ECOLOGY

Total collected (315 individuals)	\$943.93
Total expenses	
(Campaign, purchase of portrait, printing portrait, binding presentation copy)	165.54
Available for expense of printing, turned over to C. S. Gager, Business Manager of ECOLOGY	778.39

(Signed) WILLIAM S. COOPER,
Chairman

The report was accepted.

REPORT OF THE COMMITTEE ON NOMENCLATURE

The mimeographed lists of ecological terms herewith presented are in three groups: Preliminary List No. 3 (11 pp.); Revised List No. 2 (17 pp.); and Definitions of soil terms useful in ecology and needing clarification (3 pp.). The terms in the first list are given for the first time this year. The committee is indebted to S. A. Cain for the definitions of numerous terms and to the sub-committee, Joseph Kittredge, Chairman, S. O. Heiberg, H. J. Lutz, and J. T. Auten, for definitions of soil terms. Many of the terms in the Revised List appear in this report for the third time. The committee appreciates especially the valuable suggestions received from H. I. Baldwin and A. G. Vestal. It is planned to issue future reports in form similar to that of this year. Each year the terms given the preceding year in the Preliminary List will be added to the Revised List.

One of the chief aims in establishing this committee was that it should serve as a clearing house, or discussion center, of ecological terms. In order to fulfill this purpose many comments and suggestions that have been received are included in this report. In order to make the work of the committee as valuable as possible it is urged that more members and others interested cooperate by sending suggestions and definitions to any member of the committee.

It is hoped that in time the glossary can be presented in more finished form

so as to include briefer definitions, derivation, synonymy, cross-references, and equivalents in foreign languages. References have frequently been given in the report for the purpose of showing the origin of the particular definition and to furnish leads to those interested in further study of the terms. No attempt has thus far been made to give credit to the man who coined the term.

A mimeographed copy of the three lists may be obtained from the chairman. Please enclose 6 cents in stamps.

Respectfully submitted,

HERBERT C. HANSON, Botany (*Chairman*); FRANK E. EGGLETON,
Limnology and Hydrobiology; C. F. KORSTIAN, Forestry;
Z. P. METCALF, Entomology; L. E. NOLAND, Zoology

The report was approved and the committee was continued.

REPORT OF THE COMMITTEE ON NOMINATIONS

Your committee submits the following nominations:

For President: W. S. Cooper, Minnesota.

For Vice-President: J. G. Needham, Cornell.

For Secretary-Treasurer: Orlando Park, Northwestern.

For the Editorial Board of Ecology: Paul S. Welch, A. O. Weese, H. S. Conrad, and E. Lucy Braun.

For the Editorial Board of Ecological Monographs: Chancey Juday, H. C. Hanson.

For reelection as Joint Editor of Ecology for five years: Geo. D. Fuller.

For reelection as Joint Editor of Ecological Monographs for five years: A. S. Pearse.

Your committee recommends the appointment as representative of the Ecological Society on the Conservation Council, Chicago, of George D. Fuller, with W. G. Waterman as alternate.

Your committee also recommends that the more definite organization of the Pacific Coast section of the Ecological Society be given careful consideration.

G. D. FULLER (*Chairman*),
W. C. ALLEE,
G. E. NICHOLS

There being no nominations from the floor it was moved, seconded and carried that the Secretary be instructed to cast the vote of the Society for the list of officers presented by the Committee on Nominations and that the recommendations of the Committee be approved.

The vote was cast and the persons named were declared elected as officers of the Society for the coming year.

REPORT OF THE COMMITTEE ON ACTIVITIES IN PRESERVATION AND STUDY OF COMMUNITIES

The committee appointed at the Pittsburgh meeting to study the work and to recommend future activities of the Committees on the Study and Preservation of Communities, was composed of Francis Ramaley (*Chairman*), B. C. Tharp, A. H. Wright, and L. R. Dice. Its report was presented in the form of a motion that the Committee be continued with the same personnel, and with authority to the chairman to fill gaps in membership as they may occur. The motion was seconded and carried.

REPORT OF THE COMMITTEES ON THE STUDY OF PLANT AND ANIMAL COMMUNITIES, AND PRESERVATION OF NATURAL CONDITIONS

The year 1935 has been one of unusual progress in the setting aside of natural and sub-natural areas by government agencies, but also one of unusual aggression in the destruction of animals outside of National Parks. In all probability the \$1,300,000 for the destruction of birds and mammals, opposed by naturalists a few years ago, has been reached or exceeded by expenditure of the Federal Government through the usual channels, plus the various work-relief projects supported by the federal and state governments. Serious fear has been expressed by the Utah Academy that many species, cougars, bobcats, bears, wolves, etc., will be entirely exterminated from the areas adjacent to the Great Basin. The jack rabbits and kangaroo rats have been extirpated from the Santa Rita Range Reserve in Arizona, predatory hunters are busy in the bush-covered areas of Texas, and in some of the eastern states prizes have been offered for the killing of so-called vermin, including the gray squirrel, etc.

Canadian members report that the first control campaign against predatory animals is in progress in the Canadian National Parks. Some Canadian members report caribou and musk ox in need of protection, and lynx, marten, fisher, and otter in a serious position. A resolution was drafted, addressed to the Canadian Committee for the Preservation of Natural Conditions. This and other resolutions which will be found in the report of the Committee on Resolutions. Subcommittees are being constituted to pursue the objectives of these resolutions.

At St. Louis the committee met in the Blue Room of the Warwick Hotel, 8:30-9:40 A.M., Tuesday, December 31, with 20 members present. Two new items of business were introduced.

Dr. E. Lucy Braun has discovered an area of primeval deciduous forest on Lynn Fork, Perry County, Kentucky, at much lower altitude than any forest in the National Parks of the Appalachian mountains. The Committee is committed to the policy of urging the establishment of National Monuments to preserve examples of the various types of biotic communities and indorses the preservation of the Lynn Fork Deciduous Forest. A com-

mittee composed of J. M. Shaver (*Chairman*), S. A. Cain, E. B. Powers, and H. M. Jennison was recommended to examine the area and make a recommendation to the society.

Attention was called to the great reduction of prairie dog towns and the intention of the Resettlement Administration to exterminate them in grazing areas. Curator W. H. Over was nominated chairman of a committee to include Prof. Chamberlain and a committee of three to locate and urge the preservation of some prairie dog towns in South Dakota.

Due to the aggressive destruction of animals on range and forest lands during 1934 and 1935, it was requested that the Committee on the Preservation of Natural Conditions be authorized to urge the governmental bureaus to set up buffered sanctuaries (zoned natural history reserves) and to include with natural vegetation, all forms of life including carnivores, the resolutions having been adopted by the advisory board and were read and criticized at this meeting of the committee.

Old Business

At the Boston Meeting a committee to gradually classify the Primeval National Parks, the Military Historic Parks, etc., recently placed in charge of the National Park Service so as to insure the fullest protection of nature from inroads of improvements and concessions and as a guide to the quality of new additions to the National National Park and National Monument System, was appointed. It was not thought wise to raise this question during 1934 on account of the large number of new faces in Congress. The appointing of the Committee was left to your Chairman. The Committee on Preservation agreed that its personnel should constitute a part of the membership and that three other members including a Chairman, should be found. Two new members agreed to act, but a Chairman has not been found. Unless the executive committee can assist with the problem of securing an active chairman the matter will have to be dropped.

The Society in 1932 asked the National Research Council to establish a committee on the Ecology of Grasslands of North America. The committee was organized in 1933 and met in Austin, Texas, to organize a program which is concerned chiefly with the acquirement of land at well spaced study centers. The committee met again in June, 1935, at Fargo and Dickinson, North Dakota. The Ecological Society has maintained local grassland committees at the several centers, with the local member of the National Research Council as Committee Chairman, for the purpose of securing of suitable areas of grassland for study at the several study centers in cooperation with the National Research Council. President Taylor of the Ecological Society, made the following appointments of local committees:

Arizona Center

C. T. Vorhies (*Chairman*), E. D. Ball, Forrest Shreve, R. H. Canfield, C. K. Cooperrider, Wm. G. McGinnies, D. M. Gorsuch.

Texas Center

B. C. Tharp (*Chairman*), J. B. McBryde, C. W. Goldsmith, W. J. Tucker.

Oklahoma Center

A. O. Weese (*Chairman*), P. B. Sears, A. I. Ortenburger, M. W. Shackelford, C. W. Thornthwaite.

Nebraska Center

J. E. Weaver (*Chairman*), Irving Blake, George E. Condra, Myron H. Swenk.

Illinois Center

V. E. Shelford (*Chairman*), W. L. Burlison, H. J. Fuller, J. J. Pieper, R. S. Smith, M. C. Farrar, W. P. Flint, T. H. Frison, C. L. Metcalf, A. G. Vestal, R. E. Yeatter

Iowa Center

B. Shimek (*Chairman*), Jos. H. Bodine, R. B. Wylie, L. O. Nolf, W. S. Anderson, A. L. Bakke, H. E. Jaques.

North Dakota Center

H. C. Hanson (*Chairman*), O. A. Stevens, J. A. Munro, P. J. Olson.

Saskatchewan Center

K. M. King (*Chairman*), D. S. Rawson, S. E. Clarke, W. P. Fraser, H. G. Crawford, T. Stevenson.

These committees have been drafting plans for grassland acquirement at the several centers.

The committee asks that it be continued during the coming year with Dr. R. E. Yeatter, Game Specialist, Illinois Natural History Survey, Secretary of the Preservation Committee; further, that the committee with Dr. Ramaley, Chairman, be continued to advise the Society as to the reorganization of the committees at end of the year, after which the Chairman finds it necessary to take a much less active part. It is hoped that a general plan for saving a representative of the North American fauna may be prepared during the coming year.

The Chairman further asks that \$25.00 to \$50.00 of the dues income of the Society (if available) be assigned to the committee together with all contributions and the royalties from the Naturalist's Guide.

During the year 1935 the committee has used only contributions solicited by the chairman; some typing has been done by a N. Y. A. typist supplied by the University of Illinois. A bill of \$5.63 covering 1934 mimeographing and postage was paid by treasurer. The financial report for 1935 is as follows:

Receipts

From contributing Societies and individuals	
American Society of Mammalogists	\$ 1.20
New Orleans Garden Society	5.00
Wilson Ornithological Club	1.00
Kansas Academy of Science	5.00
Wild Flower Preservation Society, Ohio	1.00
Cranbrook Institute	2.00
American Museum of Natural History	10.00
Botanical Society of New Orleans	2.00
Southern Biological Supply Company	2.00
Connecticut Botanical Society	5.00
Phi Sigma, Kappa Chi, Lawrence, Kansas	10.00
C. C. Deam	1.00
J. Grinnell	5.00
E. S. Hathaway	2.00
A. H. Wright	1.00
Botanical Society of America (Due from E. S. A.)	5.00
Ecological Society, 1934, contribution and royalties	5.00
Royalties due from E. S. A.	8.00
	<hr/>
	\$71.20

Expenditures

Mimeographing	\$16.81
Reprints	3.87
Typing	15.49
Stationery	1.18
Postage	15.25
	<hr/>
	\$52.60
	\$71.20
	52.60
	<hr/>
Balance	\$18.60

Respectfully submitted,

V. E. SHELFORD, *Chairman.*

The report was unanimously adopted by the Society.

REPORT OF THE COMMITTEE ON RESOLUTIONS

Your committee offers these resolutions:

1. *Resolved*, that this Society appreciates greatly the facilities offered by the authorities of Washington University for our 1935-36 meeting, and we hereby express our sincere thanks to all members of local committees who have helped toward the success of the meeting.

2. *Resolved*, that the Ecological Society of America hereby expresses its thanks to speakers participating in the symposium on "Ecological Aspects of Recent Governmental Activities." We appreciate very much the courtesy

of the various Federal agencies involved, including the representatives of the Shelterbelt Project, Biological Survey, Forest Service, and Resettlement Administration.

3. WHEREAS, the American Committee for International Wild Life Protection has submitted the following resolution for endorsement and support of conservation and sportsmen's organizations in the United States that have an interest in preserving the wild life, especially the rare species, of foreign countries, be it

Resolved, that the Ecological Society of America endorses and pledges its support to this resolution, which is worded as follows:

"Under progressive exploitation of natural resources throughout the earth, pressure on many interesting species has been such as to bring alarming reduction in numbers or even extermination in numerous forms of both animals and plants.

"In view of this, while it is important that representatives of the fauna and flora of the world should be preserved in museums, zoological gardens and arboretums for scientific study, in future, specimens of the rarer species need to be obtained with discretion in order that collecting in the name of science may not lead to actual extermination.

"It is urged that organizations and private collectors agree to carry on zoological exploration, collecting and purchases of specimens in such a manner as not to injure or endanger the continued existence of any form. We ask the assent and cooperation of all interested agencies in this important matter."

4. WHEREAS, the National Resources Board in its recently published report has recommended that the President of the United States be empowered to declare as National Wards certain rare mammals, birds, or similar unique natural objects as for example the grizzly bear, the Florida manatee, and the trumpeter swan, and Whereas, it is the belief of the society that such action will be necessary over and above any other form of legal protection yet devised, if such species and objects are to be saved from extinction in the national interest, be it

Resolved, that the Ecological Society of America urges that appropriate legislation delegating such authority to the President be enacted by the Congress of the United States.

5. WHEREAS, furs are among the most valuable of animal products in North America, values from fur sales amounting to a large sum each year, and Whereas, flesh-eaters among mammals and birds are well-known to fill a distinct and important place in the economy of nature, although details of their relationships to other species and their environment are lacking, be it

Resolved, that the United States Government and the States and all institutions having the opportunity to do so be encouraged to make thorough studies of the life histories and ecology of the flesh-eaters, to serve as a basis for their scientific management.

6. *Resolved*, that the Ecological Society of America urges every educa-

tional institution concerned to institute courses in ecology, where these are now lacking, covering both plants and animals, and that in all practicable ways each institution inculcate and inspire a broad and synthetic point of view that will enable students to see the problems of natural resources, not as separate and discrete, but as parts of a single master problem of how best to administer nature as a whole.

7. WHEREAS, thinking persons do not wish to bequeath to future generations a purely mechanical and industrial world,

WHEREAS, the threat of insufficient food which called for the utilization of all possible land as urged by economists thirty years ago is and will be void for many generations, and economic conditions are such that it is necessary to withdraw land from cultivation and remove settlers from poor land,

WHEREAS, the larger wild animals, especially carnivores are of value in the economy of nature, and therefore of importance in the proper development of the science of ecology, which supplies information to be used in interpreting the past and predicting the future of biological events in relation to weather, etc., be it

Resolved, that the Committee on the Preservation of Natural Conditions be authorized to urge the governmental bureaus to set up buffered sanctuaries (zoned natural history reserves) and to include with natural vegetation, all forms of life including carnivores as follows:

TO THE UNITED STATES FOREST SERVICE:

WHEREAS, several of the National Parks are too small to support wide-ranging carnivores and experience has shown that they cannot be maintained in the existing parks, be it

Resolved, that the Ecological Society of America urges that the United States Forest Service cooperate with the National Park Service in protecting roaming animals in forests surrounding or adjacent to National Parks, especially Yellowstone, Yosemite, Lassen Peak, and Great Smoky. This can be accomplished only by setting aside a zone of protection for roaming animals agreed upon with the Park Service, as follows: not less than 50 miles wide around Yellowstone and 25 miles wide around the other three.

The Society further urges that the Forest Service cooperate with the Park Service in the acquirement of lands surrounding National Parks wherever possible, to be used for tree growing and other forest experiments while acting as buffers for roaming animals. In particular, acquire areas of deciduous forest surrounding the Great Smoky National Park which may serve for tree-growing experiments while acting as buffers for roaming animals. We also urge such use of forest or portions of existing forests adjacent to National Parks as buffer areas. Furthermore, we urge the enlarging of forest type areas already set apart so that they may serve as animal sanctuaries and that control measures applied to birds and mammals be kept out of these sample-plot areas and also out of a large zone surrounding each.

The Society also urges that the Forest Service set aside one or more tracts and the Idaho Primitive Area in which puma, bobcat, wolf, wolverine, otter, fisher, and marten be allowed to breed unmolested, surrounded by a second area in which breeding will be discouraged if found, and around this a third in which roaming animals will not be molested. We request consideration of the possibility of similar action in the Uintas and Wind River Range.

TO THE NATIONAL PARK SERVICE:

The Ecological Society of America urges,

That island National Parks be used as preserves for all forms of life, including wolf, wolverine, bobcat, etc., wherever they still exist.

That with the acquirement of the Big Bend Area in Texas as a National Park it be buffered about by a wide strip of other land in partial use where roaming animals are protected.

The setting up of a National Monument in the desert grassland in southwestern New Mexico or southeastern Arizona to preserve the fauna peculiar to that region in a buffered sanctuary, and perpetuate the natural flora.

The enlargement of the Great Smoky National Park or buffering of the same and restoration in so far as possible of the deciduous forest fauna.

TO THE DEPARTMENT OF THE INTERIOR:

The Ecological Society of America urges,

The setting aside of an area of desert grassland in southwestern New Mexico or southeastern Arizona to consist of not less than 150,000 acres, upon which badger, foxes, weasels, gopher snakes and other predatory animals will be encouraged in the hope of establishing a permanent system of balance between rodents and carnivores which will make for development of a permanent system of grazing. This area to be held as a check on areas treated in a different manner.

We further urge the turning over of areas of public domain to the National Park Service or Forest Service, to provide buffers for roaming animals, wherever the public domain is adjacent to the national parks.

TO THE BIOLOGICAL SURVEY:

The Ecological Society of America urges the enlargement of Wichita Game Preserve to give more grassland on which experiments should lead toward a balance between carnivores and rodents, which has a bearing on control measures for rodents and the preservation of the complete plains fauna.

The Society also urges the cooperation of the Biological Survey with the Park Service and Forest Service in affording protection for roaming animals in buffer zones surrounding the Parks.

TO THE ECOLOGICAL SOCIETY'S CANADIAN COMMITTEE FOR THE PRESERVATION OF NATURAL CONDITIONS:

WHEREAS predatory animal control in the National Parks of Canada is at its beginning,

WHEREAS the newspapers often mention the introduction of the reindeer into the Canadian tundras,

WHEREAS experience with the reindeer in Alaska includes hybridization with the native caribou, deterioration of the wild species, and its extirpation from reindeer areas,

WHEREAS indifference on the part of scientists has in the United States contributed to the extirpation or extermination of many species, and

WHEREAS no buffered reserves are known to be set up in Canada, be it *Resolved* that the Ecological Society of America suggests to its Committee on Preservation of Natural Conditions for Canada and other members in Canada to warn their government officials that the experience in the United States indicates that measures should have been taken long ago to preserve within the territorial boundaries of the United States populations of wolf, wolverine, badger, kit-foxes, etc., in buffered sanctuaries. The loss of these animals is decidedly detrimental to ecological science and to game and fur management. It grew out of optimism as to the survival of animals in small numbers in the areas where agriculture and grazing are being carried on, and

The Society further suggests to its Canadian members to advocate the buffering of the Canadian National Parks, and to warn against the introduction of the reindeer in the Canadian tundra.

TO THE CIVILIAN CONSERVATION CORPS:

WHEREAS, natural conditions in the United States are rapidly disappearing, be it

Resolved, that the Ecological Society of America regrets the activity of the Civilian Conservation Corps in opening up certain areas still in approximately natural state to the traveling public by the introduction of automobile roads and by trails, and in clearing out the natural growth and cover suitable for the preservation and continuation of our native fauna, and urges that in the future such activities be restricted to the more settled portions of the various states.

8. WHEREAS, the studies by Mr. T. K. Pavlychenko on root systems of plants are of such value that it is highly desirable that the results be made known both to students of plant science and to the general public;

Resolved that the officers of this society call attention of various Canadian authorities to the importance of publishing the material and that, in particular, such suggestion be communicated to the National Research Council of Canada and to the University of Saskatchewan.

9. *Resolved*, that the Executive Committee send a statement to governmental agencies, as the Biological Survey, Office of Indian Affairs, Forest Service, Resettlement Administration, Soil Conservation Service, National Park Service, Office of Agricultural Experiment Stations, National Planning Board, State planning boards, and other state and local governing bodies,

expressing the Society's appreciation of the difficulties involved in solving ecological problems dealing with conservation and efficient utilization of plant and animal resources, and offering our cooperation in the following ways:

Furnishing sources of facts, methods, and procedures for projects under way,

Suggesting useful projects and competent men to aid in their execution,

Offering constructive criticism of policies and projects being planned or in operation.

10. WHEREAS, in none of the articles on the shelterbelt which we have seen have the potentially important wildlife phases of the shelterbelt enterprise been given adequate attention, and

WHEREAS, these wildlife phases, involving not only forest trees, but also brush, herbs, and grasses, and birds, mammals, insects, and a host of other animal forms, are likely to be of profound significance and importance in the biotic communities involved in the shelterbelt, and

WHEREAS, we feel that if major values are to be secured the shelterbelt enterprise must be handled from a broad view of the total community of plants and animals, on an ecological basis, rather than from a silvicultural or botanical standpoint alone, therefore be it

Resolved, that the Ecological Society of America hereby recommends to the United States Department of Agriculture a detailed and thorough study of these wildlife phases, with the objects of (1) Anticipating the effects of the shelterbelt on the insect, bird, and mammal life and other animal phases of the shelterbelt and neighboring areas (2) Making the most of the enterprise from the standpoint of game bird, mammal, and fur-bearing mammal production (3) Managing the areas in such a way that the killing of plant-consuming species of animals or of flesh-eaters will be reduced to a minimum, and (4) so administering the entire project that maximum values on a permanent basis may be secured from all phases of the enterprise.

11. WHEREAS in the present expansion of planting activity, a large number of species of trees and shrubs are used for reforestation, food for wild life, as protection against wind and water erosion, and as shelter from wind, which have heretofore been little used, and about whose artificial propagation little is known, and

WHEREAS the use of such seeds involves their collection, extraction, and storage on a large scale, with danger of seeds being obtained from sources differing widely from the proposed planting site, leading to possibility of introduction of unsuitable races, and

WHEREAS no adequate facilities exist at present for basic research and testing of forest seeds in spite of the urgent need for testing and control of origin of such seeds, be it therefore

Resolved that the Ecological Society of America, recognizing the importance of fundamental research on tree seeds and the influence of different races, recommends the establishment of a central tree-seed testing station

and that the secretary be requested to transmit a copy of this resolution to the council of the A. A. A. S. and to other agencies as may be considered appropriate.

All of the above resolutions respectfully submitted.

C. T. VORHIES,
FRANCIS RAMALEY (*Chairman*)

Each of the resolutions was adopted individually by the society. The sixth, on ecological teaching, was referred to the Society's members for their efforts in their own institutions. The committee was commended for the volume of its accomplishment in very limited time.

As part of an interested discussion on the programs of the winter meetings, Dr. C. C. Adams moved that a committee be appointed to consider organization of sections within the society, covering special divisions of ecology, affording those divisions increased opportunity at the annual meetings, and attracting as new members individuals who are interested in those divisions. Divided sessions running concurrently may afford relief from the too crowded character of some recent meetings. Additional joint sessions with other societies, and other ways of increasing the value of the programs, are also to be considered by the committee. The motion was seconded, and unanimously carried.

The meeting was adjourned at 1:15 P.M.

A. G. VESTAL, *Secretary*

NOTES AND COMMENT

EQUIPMENT FOR THE STUDY OF AQUATIC ANIMALS UNDER CONTROLLED CONDITIONS OF TEMPERATURE AND LIGHT

NEVILLE L. BENNINGTON AND GLENN C. DILDINE¹

Northwestern University

An increasing amount of analysis is being carried on influences controlling reproductive cycles in animals, *e.g.*, Rowan (1929), Bissonnette (1935), and Wells (1935). These workers find that light and temperature are basic influences. Since experimental modification of reproductive cycles in fishes has received scant attention, the authors have evolved equipment controlling light and temperature, suited not only to the study of fishes but also to many other aquatic animals. The general applicability of the apparatus suggested this publication, and the paper will also serve as a basis for future reports on experimental work already done or now in progress. Since the various units of the equipment are similar to many in general use, any claim to originality must rest on their assembly as a whole.

APPARATUS

General Description

Basically, the apparatus (Fig. 1) consists of a vertical series of three long, shallow, galvanized iron tanks (1), each six inches by fifteen inches by seven feet, providing ac-

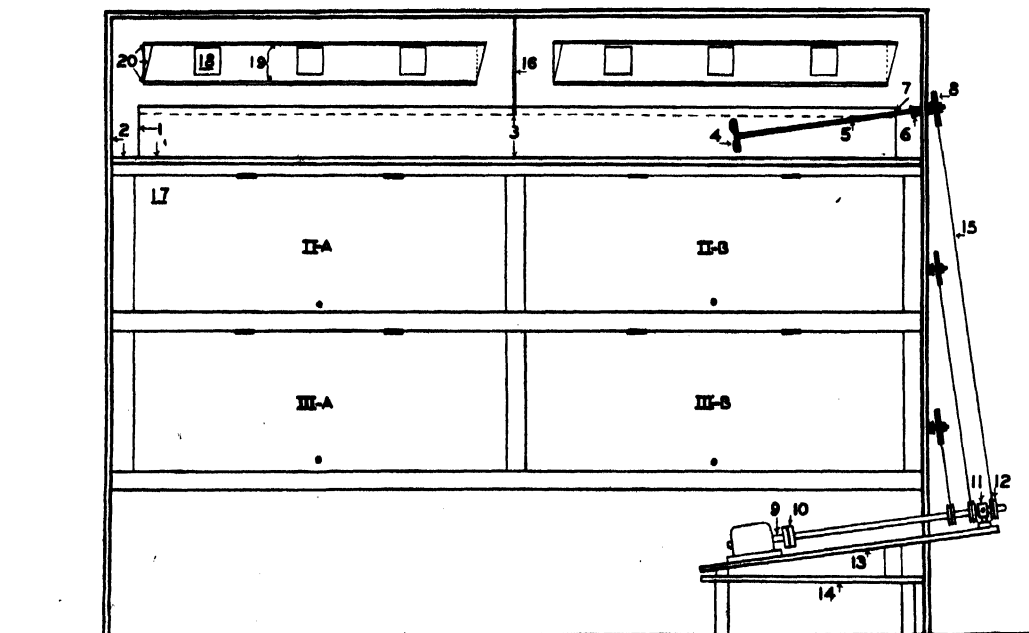


FIG. 1. Side view of whole assembly. Top tank (I) in median section to show stirring and light control units; tanks II and III with doors closed.

¹ The authors are indebted to Dr. C. L. Turner, Dr. J. W. Buchanan, and Dr. W. R. Duryee for helpful suggestions, and to Dr. Orlando Park for criticism of the manuscript.

commodation for sixty glass, liter aquaria. The supporting framework (2), of one and one-quarter inch pipe, holds each successive tank twenty-two inches above the one below. Drains are arranged in each tank to maintain a water depth (3) of approximately five inches, deep enough to partially cover aquaria or other containers holding the experimental animals. Control of the water temperature in the three large tanks, in which the aquaria are immersed, serves to maintain a uniform temperature in aquaria in any given tank. It is thus possible to provide habitats at three different temperatures. From top to bottom, the three tanks are kept respectively at 18° – 19° C., 23° – 24° C., and 28° – 29° C.; these upper and lower limits are just within the survival limits of some of the fish which have been used.

Temperature Control Mechanism

Constant temperature is obtained in each tank by a balance between cold water intake and a heating element submerged in the tank. This element, a Cenco knife-blade heater, is regulated by the common circuit (fig. 2). This includes a bimetallic thermostat (1) which is immersed in the tank and connected through an eight to twelve

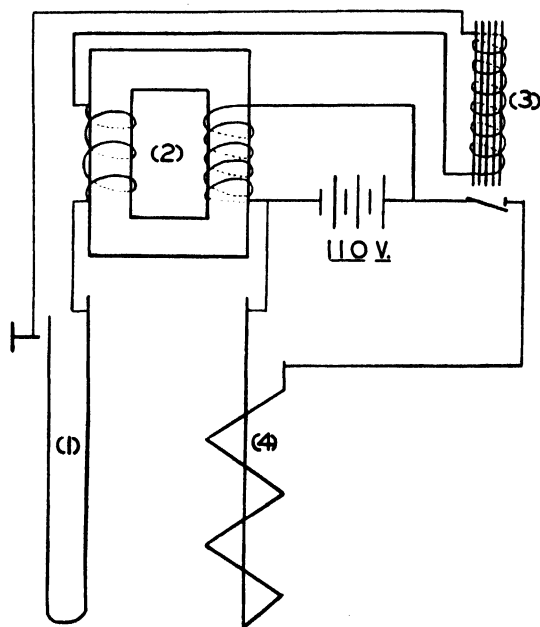


FIG. 2. Wiring diagram to show connections of thermoregulator (1) through eight volt current (bell transformer (2)) to mercury switch relay (3) and knife blade heater (4).

volt current which is secured by a bell transformer (2). This current activates a mercury switch relay (3), which turns on the heating element (4). The bimetallic regulator is of the coil type, with silver electrodes. Both the thermoregulators and the mercury relays (except for the Mercoid tubes themselves) were constructed by the authors. A two micro-farad condenser placed across the contacts of the thermoregulator materially decreases the arcing at break, thus decreasing point corrosion and attendant loss of contact. With proper attention, the temperature remains constant within one-quarter of a degree C.

In tanks as long as these, it is obvious that a stirring device (fig. 1, upper right) is necessary to maintain uniform temperatures throughout each tank. For this purpose,

three and one-half inch propellers are fitted into each tank, all three at the same end of the assembly. Each propeller blade (4) is cut and fashioned from copper sheeting and soldered to the inner end of a twenty-four inch shaft (5) of steel curtain rod. The outer end of the shaft, threaded to fit the cones of a bicycle front axle, is mounted through a bicycle front hub (6) which serves as a ball bearing for the rotation of the propeller shaft. This shaft runs through a hole (7) just above the water line in the end of each large tank. The hub is mounted outside the tank, at such an angle that the propeller inside the tank is totally submerged when rotating, but still pushes water toward the far end of the tank, rather than downward against the bottom. A four inch pulley (8) is fastened at the outer end of the shaft, where it projects beyond the hub.

Power for the propellers is supplied by a one-quarter horse power induction motor assembly (Fig. 1, lower right) utilizing standard power tool equipment. The motor shaft (9) is mounted, through a universal joint (10), directly in line with a shaft eighteen inches long. The opposite end of this accessory shaft is supported by a small bronze bearing (11). Three two inch pulleys (12) are mounted on the accessory shaft. The whole motor and shaft assembly is mounted in rubber on a board (13) which is also rubber-mounted to a stationary table (14) at the side of the tanks, insuring quiet operation. The motor and shaft assembly is so placed that belts (15) connect each of its three pulleys to the appropriate propeller shaft pulleys (8). This equipment is still in good condition after continuous operation for five months.

Light Control

In most of the experimental work so far one side of each tank (A—I, II, III) is dark, and the other side (B—I, II, III) is illuminated by sixty watt bulbs. In order to control light admitted to the tanks, the whole series of three tanks (Fig. 1, upper left) is enclosed by wallboard. Each tank is divided into two equal compartments by a median crosswise partition (16) extending down to the top of the water. Separate doors (17) are fitted to each of the six resulting compartments. On the opposite side or back of each compartment three four by five inch windows (18) penetrate the wallboard. Outside each window a lamp socket is fastened on a ledge which is so tilted that each bulb projects through its window and partly into the compartment. All bulbs are insulated from the interior of the compartments by glass plates (19) mounted at an angle (20) to the wallboard. This insulation is a necessary precaution, since the lights are turned off at night and on in the morning. Without insulation the added heat during the day would necessitate a daily change in the cold water intake.

Oxygen Concentration

An outside source is needed to maintain normal oxygen concentration in dark tanks. To supply oxygen without plants, an air compressing pump has been added to the assembly.

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ABUNDANCE AND DIGGING RATE OF POCKET GOPHERS,
GEOMYS BURSARIUS

CARL O. MOHR

State Natural History Survey, Urbana, Illinois

AND

WM. P. MOHR

Rapidan, Minnesota

A census of pocket gophers, *Geomys bursarius* (Shaw), at Rapidan (Blue Earth county), Minnesota, revealed a population of eight individuals on 1.46 acres of natural prairie: a rate of 5.5 to the acre during early October, 1934.

Before trapping we counted all visible mounds amounting to 303 thrown out by these eight gophers and compared them with 1652 visible mounds thrown out on ten acres of adjacent natural prairie. (Vegetation completely covers mounds within two months but the rate of coverage varies with soil, precipitation and kind of plants present. The areas under consideration are apparently uniform in these respects). In this way we estimated that 44 gophers were at work on the area or a rate of 4.4 to the acre.

A census of an alfalfa field of three acres during August 1929 yielded 13 individuals or a rate of somewhat more than four to the acre. Within five days after a light rain these gophers threw out an average of 1.58 mounds each daily and during the same period, 581.44 mounds were thrown out on a nearby 16-acre field of alfalfa. We, therefore, judge that this field was populated at the rate of 4.6 gophers to the acre.

A third census, also on three acres of alfalfa, yielded 18 individuals or a rate of six to the acre between May and September in 1934. This rate would undoubtedly have been higher if all of the trapping had been properly accomplished at the end of the breeding season.

A census of Illinois representatives revealed five individuals on 0.15 acre at Kappa during the second week in October 1935. An estimate based upon these data is remarkably high and is undoubtedly in the nature of *greatest density* as defined by Elton ('32, '33, p. 51). This colony like many in Illinois (Mohr, '35) was confined to a strip four meters wide between a concrete highway and farmland. Inhabitable but unoccupied sod extended 400 meters northward on both sides of the highway and furnished 0.93 acres of additional range. This is probably all used during the course of a year. (The colony did shift 80 meters northward in one month). If, on this evidence, the total available ground surrounding the colony is used in calculations, we arrive at an estimate of *economic density* which is somewhat more than four individuals to the acre and which is close to our other figures.

Other writers have estimated populations at from three to four per acre on prairie in the Mississippi watershed (Bailey, '65, p. 16) and 10 to 15 per acre, presumably under clover and alfalfa, in Iowa (Butcher, '29, p. 13). Neither stated the time of year of his observations.

RESTING GROUND

Inhabitable but unoccupied ground between groups is more obvious in the case of pocket gopher, prairie dog and similar colonies than among wider ranging mammals. Such ground is not to be confused with blanks or relatively uninhabitable areas. It is, on the other hand, ground which is vacated for a short time but likely to be used again by the same individuals which vacated it, by neighboring individuals or by immediate offspring from them within a year of desertion. In the case of pocket gophers, such

areas begin existence as thoroughly burrowed and relatively denuded ground marked by badly weathered mounds. In the case of prairie dogs, *Cynomys gunnisoni* (Baird), resting areas begin existence as deserted "towns." Taylor ('24, p. 12) states that towns are occupied continuously until the vegetation is used up and that through the western states there exist great areas of choice range land on which the vegetation has been completely destroyed by the dogs. The margins of these areas usually show a series of prairie-dog towns gradually encroaching upon the untouched grassland. The grazed areas are gone over again and again so that by the time they are deserted there is often not one small shoot left.

The population of such a town is about 25 individuals to the acre (Taylor, '24, p. 5 and Seton, '20, p. 54). This is a greatest density figure. The economic density can be calculated for prairie dogs as for pocket gophers by inclusion of resting areas in the calculations.

The function is, in part, to allow new growth of food plants, reconsolidation of the soil and possibly to allow disinfection and reduction of excreta. For this reason, it may be designated as resting ground.

Resting ground of the Illinois pocket gophers was particularly evident because the colony was forced to live on very narrow strips and therefore used the entire width. Any expansion was linear or in two opposite directions making uninhabited ground compact and easily measured. This constituted eighty-six per cent of the area apparently given over to this colony by adjustment of populations.

Resting ground was equally obvious but more difficult to measure in the other cases because the areas studied were generally wider than required by the burrow systems of individual gophers. Our method began with a calculation of areas of rectangles or triangles which closely bounded each group of new mounds. The sum of these areas was then deducted from the total area censured. In this way ninety-seven per cent of the alfalfa field was found at rest in 1929 when occupied at the rate of 4+ gophers to the acre. Some of this resting ground was well covered with alfalfa but much of it was greatly denuded.

LIVE WEIGHT

All gophers were trapped and weighed between April 29 and October 21 while young were active, growing rapidly, and perhaps being eliminated by death. Naturally, the later the catch after the breeding season the greater was the average weight. Six trapped before May 14 averaged 255 grams; thirteen caught between August 7 and 18 averaged 234.61 grams; ten caught between August 20 and September 9 averaged 240.90 grams; and six caught between September 20 and October 8 averaged 350.42 grams. The smallest individual was one of 127 grams caught August 10 and the heaviest was one weighing 481.93 grams caught May 4, both at Rapidan.

Weights per acre were as follows: on natural prairie by trapping during early October 1934, 1752 grams and by estimate from 10 acres 1576 grams; under alfalfa during August 1929 by trapping, 938.44 grams.

RATE OF HILL CONSTRUCTION

Bailey ('29, p. 13) once counted the hills thrown out by three gophers twelve days after a rain on August 2 and found the number respectively 28, 35 and 40 which gives an average daily rate of 2.86 per gopher. We found that 13 gophers under alfalfa on black loam threw out an average of 1.58 hills per individual daily during five days following a light rain at Rapidan. During 5 days following August 9, seven gophers threw out a rate of 1.88 mounds per individual each day. The average of these figures is 1.77 mounds per individual per day, all under alfalfa on black loam with clay subsoil.

At Iona, Minnesota, the junior author found a single gopher at work on July 23.

This individual threw out 11 mounds in 8 days or a rate of 1.38 mounds per day. One morning it threw out 3 small mounds.

During the last week in August, 1935, the senior author marked mounds belonging to seven individuals on natural prairie and found that, during the next 120 hours they threw out an average of 1.56 mounds. The rate of mound construction varies with the kind of food available, the season, age composition of the gopher population, amount of soil moisture, and nature of the soil. Gophers frequently do not throw out mounds during the day following long or heavy rains.

METHODS AND HABITATS

The natural prairie referred to above is, of course, not as natural as could be desired, being the type found along railroads. It had not been burned over in at least ten years, but was frequently cut for hay although not in four or five years. It was distinguished by good numbers of native yellow cone flowers, *Lepachys pinnata* (Vent.); lavender bergamot, *Monarda fistulosa* (Linn.); blue joint grass, *Andropogon furcatus* Muhl., introduced sweet clover, *Melilotus* sp. and others.

Censuses by trapping were carried on until no new mounds were thrown out during two weeks following cessation of trapping.

SUMMARY

By trapping of given areas and by comparison of digging rates we estimate that pocket gophers averaged between four and 5.5 individuals to the acre on natural prairie during early October. This is soon after the breeding season and therefore before populations drop to their annual low. The rate under alfalfa was as high as six to the acre.

Much of the ground between colonies is temporarily unsatisfactory because of denudation, etc., but must be considered in making calculations of economic density. The function of such resting ground is in part to permit new growth of food, reconsolidation of soil, and possibly disinfection and reduction of excreta.

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QUANTITATIVE LITTER SAMPLING

A new contraption for extracting arthropods from litter samples has recently been described.¹ This apparatus is claimed to work at 90 per cent efficiency in half an hour,

¹ **McClure, H. Elliott.** 1935. A soil surface sampler. *Ecology* 16: 666-669.

that is, securing a maximum of 4000 arthropods in square foot samples. Three years previously an experienced worker² found that former samples recording 20,000 individuals per square meter was only 10 per cent accurate, due to too rapid drying. A fundamental principle in such extraction is to give the fauna time enough to crawl through the material to drop through the sieve. Another is that thin skinned animals very quickly die of desiccation, thus the hot blast of the new sampler is lethal to a large part of the population. Trägårdh found that it required one or two weeks to get the fauna out of his litter samples at room dryness and that artificial heat was lethal. In other words, carefully checked experiments by an experienced Acarologist finds artificial heat is highly inadvisable. McClure checks his results by "examination" of the sample. If these samples were examined with magnification of less than $\times 20$ (Trägårdh advises $\times 30$) on anything but a dark blue ground, the estimate is erroneous. In the southern Appalachians, where litter varies from one to two inches in depth, my minimum catch was 4000 while the maximum reached 12,000 individuals per square foot. Yet only 10 per cent of the species of the immature mites were secured. Thus McClure's apparatus was below 50 per cent accurate for securing the arthropods. Furthermore he wasted a great deal of time in sorting his debris. Why not use a series of finer screens (as will be described in the next ECOLOGY)? Perhaps the most wasteful process is to be compelled to crank the apparatus for half an hour, while in the old-fashioned method no cranking or other time consuming process is needed. If the operator wishes to save time, why can he not take the sample two or three days earlier, or a week earlier, and let the fauna take all the time it needs to get below?

A really simple, portable apparatus has already been described.³ For quantitative sampling, lots should be brought to the laboratory in containers which will not lose moisture or some individuals will die of desiccation. Placing the paper bags near a radiator to dry, kills a good per cent of the microarthropods so that they never get into the sample. As the finest debris is as fine as the smallest mite, I do not understand how McClure's "screen debris sack" separates the two.

Finally letting the mites fall in alcohol causes them to die contracted instead of expanded, and it is therefore impossible to identify them. Better have them fall in a dry vial and kill "hourly" with a teaspoonful of boiling alcohol. If they die from desiccation in the vial they die partly expanded.

This is a case where scientific investigation cannot be hurried without falling from the realm of Science.

ARTHUR PAUL JACOT

APPALACHIAN FOREST EXP. STATION,
ASHEVILLE, N. C.

NOTES ON ALTITUDINAL DISTRIBUTION OF RATTLESNAKES

An altitudinal zonation comparable with that of most plants and animals has been observed with respect to rattlesnakes. These observations were made near Tucson, Arizona, principally in the Santa Rita, Santa Catalina, Tucson, and Tortolita Mountains. These notes include about 40 records of desert diamondbacks (*Crotalus atrox* Baird and Girard), 6 tiger rattlers (*C. tigris* Kennicott), 7 members of the species *C. scutulatus* Cope, and 9 blacktail rattlers (*C. molossus* Baird and Girard).

Members of three of these species—*C. atrox*, *C. molossus*, and *C. scutulatus*—seem to

² Trägårdh, Ivar. 1932. Studier över Insamlingstekniken vid Undersökningar över markens Djurliv, Meddelanden från Statens Skogsförsöksanstalt 27: 21-68. 14 figs. German abstract. Also: —. 1933. Methods of automatic collecting for studying the fauna of the soil. *Bull. Ent. Research* 24: 203-214. 8 figs.

³ *Science* 76: 299-300 (September 30, 1932).

occupy rather definite zones in a given locality, whereas those of *C. tigris* were observed to have a wider distribution. On the outwash slope northwest of the Santa Rita Mountains, the following altitudinal distribution was noted: Desert diamondbacks were found commonly at an altitude varying from 2,800 feet in the Santa Cruz Valley to an upper limit of 3,400 feet on the better grassed areas and to as high as 4,000 feet on brushy areas where grass was scanty. A winter den of this species, which has been occupied for at least the last four winters, is located at an altitude of 3,700 feet. Members of the species *C. scutulatus* were found most commonly on the better grassed areas at elevations ranging from 2,800 to 4,500 feet. The blacktail rattlers were found mostly in canyons at an altitude varying from about 4,200 to 4,800 feet where oaks and other trees furnished a fair amount of shade.

The tiger rattlers occurred in areas occupied by all the other species considered, and almost invariably in rocky districts having rough topographic relief.

Observations made in the Santa Catalina, Tucson, and Tortolita Mountains, although not so complete for all the species, seem to support those made on the Santa Ritas.

Although members of all four species may occur outside the zones of their maximum abundance, these occasional exceptions are to be expected, and they do not in any way contradict the general zonation noted.

ROBERT R. HUMPHREY

SOUTHWESTERN FOREST
AND RANGE EXPERIMENT STATION,
TUCSON, ARIZONA

COMMENTS ON THE STEM-COUNT METHOD OF DETERMINING THE PERCENTAGE UTILIZATION OF RANGES

In the July, 1935, issue of *ECOLOGY*, Stoddart¹ presented a method for determining percentage utilization of grazed ranges asserting that it is sufficiently accurate, rapid and simple for practical purposes. Briefly the method advocated is to count the grazed and ungrazed stems of the key grass species on a series of plots: divide the number of grazed stems by the total number of stems and multiply the quotient by one hundred. This method presupposes reasonably complete removal of the herbage from each stem grazed, which, according to the observations of the writer, is not the case under normal grazing conditions unless percentage utilization is uniformly heavy. If Stoddart's basic assumption of complete removal is not consistently true, results from the application of the method are unreliable, especially for the lower intensities of utilization.

Since, in connection with grazing studies, the Intermountain Forest and Range Experiment Station is interested in more accurate and simple methods for determining degree of utilization, Stoddart's method was carefully tested under field conditions to determine its accuracy and to compare it with other methods already in use.

An area on the spring-fall range of southern Idaho where thickspike wheatgrass, *Agropyron dasystachyum*, is predominant was selected as a location for the study. This grass is similar in growth form to bluestem, *Agropyron smithii*, upon which Stoddart conducted his study.

Two areas, naturally grazed, were first visited to study carefully the manner in which grazing animals remove herbage from this grass species. Two meter-square quadrats were established on the grazed areas. On each quadrat information was recorded as to the number of grazed and ungrazed thickspike wheatgrass stems, the average height of the grazed and ungrazed stems, the range in height of the grazed stems, and an ocular estimate of the utilization on each quadrat. These data are presented in table I.

¹ Stoddart, L. A. 1935. Range capacity determination. *Ecology* 16: 531-533.

TABLE I. *Naturally grazed meter plots*

Plot	Stem-count			Ocular util. estimate	Average height in cm.		Range in height grazed, cm.
	Ungrazed	Grazed	Util. per cent		Ungrazed	Grazed	
1	94	501	84	40	18.1	11.2	5-26
2	43	639	94	60	12.2	7.9	2-19

From table I, it is clearly evident that grazing animals do not completely utilize every stem grazed. On quadrat 1, ocularly estimated to be utilized to approximately 40 per cent and calculated by stem count to be 84 per cent utilized, grazed stems averaged 11.2 cm. and ranged from 5 to 26 cm. in height. The minimum height to which it is commonly accepted that livestock are able to graze a plant under normal conditions is 2.5 cm. Thus on the grazed plants an average of 8.7 cm., ranging from 2.5 to 23.5 cm., of usable herbage remained unutilized. Since the average height of the ungrazed plants was 18.1 cm. it may be assumed that the original usable height of the grazed plants averaged not less than approximately 18.0 cm. In all probability, therefore, not more than half the original usable volume of the grazed plants had been removed.

After ascertaining that removal was not complete on grazed plants, four plots each 1 square meter in size were selected on an ungrazed area to test in more detail the accuracy of the stem-count method for this type of range. Each plot was divided into five equal strips to be treated as units. From 180 to 250 thickspike wheatgrass plants occurred on each unit. Four systems of determining utilization were used: volume removed, height removed, ocular estimate of volume removed, and the stem-count system. Before clipping, the average height of thickspike wheatgrass plants on each unit was recorded. Removal was then conducted artificially with shears, every effort being made to simulate actual grazing. The portion removed was segregated by units and placed in a sack. Each unit was clipped to a different intensity, ranging from 10 to 75 per cent.

After clipping, average heights were again measured, grazed and ungrazed stems were counted, and volume removal was estimated by each of three individuals. After these data were secured the thickspike wheatgrass plants on the units were all clipped to 2.5 cm., herbage being segregated by unit. Both sets of herbage samples were then air dried for several days and weighed.

Percentage utilization or removal was then calculated using the following formulae:

$$\text{Percentage by height} = \frac{\text{Aver. height before grazing} - \text{aver. height after grazing}}{\text{Aver. height before grazing} - 2.5 \text{ cm.}} \times 100.$$

$$\text{Percentage by volume} = \frac{\text{Weight herbage removed (first clipping)}}{\text{Weight herbage removed (first clipping) + weight remaining herbage clipped to 2.5 cm.}} \times 100.$$

$$\text{Percentage by stem-count} = \frac{\text{No. grazed stems}}{\text{No. grazed stems} + \text{No. ungrazed stems}} \times 100.$$

Results are presented in table II. Significance was tested by means of Student's "Z" method.

As shown in table II the stem-count was the only method which differed greatly from the actual percentage of volume removed. Odds are 9999 to 1 that the difference of 28.7 per cent between the means of the actual volume removed and the stem-count method is significant. Since odds of 100 to 1 are usually considered statistically significant, it is safe to assume that the large difference between the stem-count method and

TABLE II. *Artificially grazed plots. Summary of 20 units. Utilization percentages by different methods*

	Volume (Check)	Stem- count	Measure- ment	Ocular by individuals		
				1	2	3
Percentage utilization	41.35	70.05	42.10	39.00	42.50	41.75
Difference		28.70	.75	-2.35	1.15	.40
Odds of significance		9999	2.00	8.68	2.00	2.00
Range in difference		13 to 53	-27 to 16	-20 to 17	-15 to 18	-20 to 26

actual volume removed is real and is not due to chance. In comparison, odds are very low (less than 10 to 1) that the differences between the means of the measurement method or the ocular estimate method and actual volume removed are significant. The data show that these two methods, as indicated, closely approximate the actual volume removed. With the stem count method on a unit unclipped except for a few plants the difference was only 13 per cent, whereas on another unit, lightly but uniformly clipped, the difference was as great as 53 per cent. Differences, however, were consistently positive; that is, the percentage utilization derived from the stem-count method in all cases was higher than the actual volume removed. These differences are largely all due to the fact that the stems grazed were not completely utilized. Because complete removal is the premise upon which the method is based its mechanics are at fault.

Ranges in differences of the measurement and ocular methods are equally as great as that of the stem-count method, but since the errors lie in personal estimates rather than the mechanics of the method they tend to be compensating and can be corrected.

According to these data the stem-count system of obtaining percentage utilization is not of sufficient accuracy to merit its unqualified use in pasture or open range studies. It is theoretically unsound since it is based on the premise that each individual stem is completely removed by grazing. Since this is not the case, all deviations or errors are positive and cumulative. Errors inherent in other methods used are frequently as great but tend to be compensating in nature.

JOS. F. PECHANEC

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WHAT IS ECOLOGY AND WHAT GOOD IS IT?¹

WALTER P. TAYLOR

U. S. Biological Survey, College Station, Texas

A prominent member of the American Association for the Advancement of Science is reported to have said that he and his wife had never in their lives disagreed about anything, although he conceded that sometimes it took them a whole evening to define their terms. Here is a hint for ecologists. It seems to me a good deal of discussion in the ecological field and much of the comment upon and criticism of it by those who do not call themselves ecologists result from a failure to agree on what ecology is.

One does not go far in the study of definitions of ecology before he realizes that, as a rule, the content of the definition depends to a considerable extent on the field in which the writer is at work. According to a student of plants, ecology is perhaps very little more than a branch of botany. The zoologist is likely to think of ecology as animal ecology. Some of the physiologists have defined ecology as a part of general physiology, while others have regarded the two as identical. A forester is quite likely to think exclusively of forest ecology. One range ecologist defines it as the relation of invasion and succession to range management. Geography and ecology recently have been used as near synonyms. A number of workers regard ecology as the science of communities. There are other definitions: One writer thinks of ecology as the science of the responses of organisms to the factors in their environment. Still others, taking a cue from the Greek word from which the first part of the term is derived, define ecology as the study of the home life of organisms.

Let us inquire a little more particularly—Is ecology a science in its own right, or it is merely a point of view?

Webster's International Dictionary regards science as "Knowledge of principles and causes" and again "Accumulated and established knowledge, which has been systematized and formulated with reference to the discovery

¹ Address of the President of the Ecological Society of America, St. Louis meeting, Tuesday, December 31, 1935.

of general truths or the operation of general laws," and once more "Any branch or department of systematized knowledge considered as a distinct field of investigation or object of study; as the science of astronomy, of chemistry, or of mind."

If these definitions are accepted ecology must certainly be regarded as a science. It must be admitted, however, that the boundaries of this science are a little hard to delimit.

When we stop to think of it we must recognize that the same difficulty arises in every comprehensive science. Adams ('13, p. 20) reminds us of the following significant incident: A university professor began a lecture on physics as follows: "Physics is the science of matter and energy. This field is so large that it is customary at present to break off the physics of the molecule and its reactions and call it chemistry. Also to put to one side the physics of the heavenly bodies and call this a part of astronomy."

In somewhat the same way we can say that ecology is the science of relations of organisms to their environment. The field is so large that it is customary at present to break off the study of plant relations to their environment and call it a part of botany, also to put to one side the ecology of animals and call it a part of zoology, the ecology of human beings and call it sociology—and so forward down a long list of fields in which the ecological approach is important.

Even chemistry, it appears, is sometimes difficult to delimit. For example, Noyes ('35, p. 358) writes that the way forward in chemistry "... is not that we shall think of it as an isolated branch of science and as independent of the rest of our lives. The days when isolation and 'rugged individualism' were appropriate are passed." "... Chemistry is not an isolated science with sharp lines separating it from physics and biology or even from economics, sociology and political science. We should see clearly," says Noyes, "that we live in surroundings that are, in reality, a *universe*, in which each part has relations with every other and that we ignore these relationships at our peril" (l. c., p. 360). If this assertion can be made of chemistry, how much more of ecology! The notion that any of the sciences is sharply set off from the others in a watertight compartment is misleading and decidedly not in accordance with the facts. A so-called individual science is merely one of the gateways to *universal knowledge*.

There is, of course, some excuse for cutting up Nature into pieces, the abstracted aspects of reality we call by such names as botany, zoology, taxonomy, physiology, chemistry, psychology, etc. The whole is too big for any one of us to comprehend. But while we do this, let us not forget that this process of analysis is merely for our convenience. Its object is to help us to better understand the whole. To a great extent we have acted as though analysis were an end in itself, that specialization is the highest good. Not so! Analysis acquires true significance only through synthesis, and specialization through the enlightening generalizations to which it leads.

"There is as much need today for a Declaration of *Interdependence* as there was for a Declaration of Independence in 1776," says Secretary of Agriculture Henry A. Wallace (*Arizona Daily Star*, Nov. 29, 1935), doubtless referring to economics and international relations. There is, it seems to me, equal need for a declaration of interdependence among plants, animals, and their environment. Such a declaration may well be the preamble of the ecological constitution.

Modern ecology owes a great deal to Möbius ('83, p. 723) who first clearly emphasized the biotic community under the term Biocoenosis: "... a community where the sum of species and individuals, beings mutually limited and selected under the average external conditions of life, have, by means of transmission, continued in possession of a certain definite territory." And note the following, also quoted from Möbius: "... if, at any time, one of the external conditions of life should deviate for a long time from its ordinary mean, the entire biocönose (sic), or community, should be transformed. It would also be transformed, if the number of individuals of a particular species increased or diminished through the instrumentality of man, or if one species entirely disappeared from, or a new species entered into, the community" (Adams, '13, p. 7).

This line of reasoning with reference to community organization is as true today as it was fifty-two years ago.

Note some of the implications. Anything that happens in any part of the world is likely to affect organisms in other parts. The extermination of a species, the depletion of soils, the deforestation of a landscape, the introduction of detrimental or valuable species of plants or animals, is likely to initiate biological, sociological, economic or political repercussions which will be felt all over the earth. Have not some recent events tended to confirm this view?

The argument for conservation is immensely stronger if it be remembered that when a normally abundant species becomes scarce or extinct many other forms are somewhat influenced. It is not alone that a gap is left. It is true that there is a void where the species formerly was, but still more serious, the entire biotic community is affected, and sometimes the inorganic environment as well. We cannot exterminate or introduce a species without far-reaching effects on other forms.

But let us refer back to our definition. It seems to me that a satisfactory definition of ecology must be big enough to take in *all* relations of *all* organisms to *all* their environment.

Ecology is not confined to animals, neither is it limited to plants. Indeed ecology is not a restricted subject. In its very essence it is comprehensive. Its stimulating key words are, integration, *Einheit*, correlation, coordination, synthesis. There is a pronounced tendency toward the replacement of restrictive definitions with more inclusive ones.

Ecology emphasizes the web of life concept. As has been pointed out in the literature ecology is "organistic," "holistic," "emergent," in its outlook.

It takes for one of its objects of particular interest and study the organism as a whole in its environment. But it goes a step farther than this, for it is increasingly emphasizing the *plant-animal community* as a whole in its surroundings.

In field investigation ecology puts the emphasis on the *quality of relations* discovered (Adams, '13, p. 33) rather than on quantity or even variety of specimens collected. Doubtless one could learn something about mechanical objects by amassing great series of bolts and nuts and steel plates and pieces of glass, but in order to build an automobile he would have to bring selected bolts and nuts and steel plates and pieces of glass into right relations with each other. Have *relationships*—of genes in the chromosome, of cells in the body, of individuals in the group, of groups in the great world biotic community, of organisms on one side and environment on the other—have these relationships and their quality been sufficiently stressed? There seems to be a growing feeling that they have not—that we have spent perhaps too much time on amassing the “blizzards of data,” as Hutchins has said, gathering much specialized information about each unit, and too little on the synthesis which alone will give meaning to the facts in hand.

The man who is sick and in need of medical attention needs a physician who can see his difficulties as a whole. It is disturbing to consult two or three specialists in as many different organs of the body and to be given a regimen for the improvement of each which cannot possibly be carried out in view of what has been prescribed already for the others. Some master practitioner must harmonize the various proposed cures or the sufferer is headed for difficulty.

I like to think of ecology as a sort of master diagnostician who tries not to lose sight of the fact that Nature, the patient, is not an accidental collocation of independent and unrelated objects, but is normally an organized and functioning whole.

Ecology, while yielding to none in its appreciation of analysis, and insisting on learning everything it possibly can through analytical processes, nevertheless stresses the indispensability of synthesis. Furthermore, the definition of ecology based on the derivation of its roots, “the science of the home life of organisms” suggests the impossibility of getting a complete picture through laboratory methods alone. In order to learn something about the home life of organisms we have got to study them in their homes.

Ecology is concerned with the world of *life* in its environment. While it recognizes differences in plants and animals, it notes also a highly significant similarity in living matter. Seemingly more and more workers in the field—especially in the United States—are impressed with the artificiality of the harsh line which is so often drawn between animals and plants. Many ecologists will vigorously dissent from Tansley's dictum that “The concept of the ‘biotic community’ is unnatural because animals and plants are too different in nature to be considered as members of the same community.” Even

Tansley, immediately following the above statement, writes: "The whole complex of organisms present in an ecological unit may be called the *biome*."

A few years back I had occasion to go over the catalogs of more than twenty forest schools in some detail. There were plenty of courses in plant ecology, and a sprinkling of animal ecology, but almost none could be found which frankly embraced both plants and animals. In at least one university there were courses in plant ecology, animal ecology, and forest ecology!

Nor could I gain information from the catalogs that indicated any attempt to coordinate or correlate the courses in ecology that were offered in the different departments.

Seemingly, the ecological point of view has not, to any extent, affected the curricula.

Are not truly ecological or bio-ecological courses needed, courses that will enable the graduate, whether he becomes a higher-up in the Washington office or a member of the supervisory and facilitating personnel of a CCC camp, to avoid wasteful conflicts? To see his problems as the wholes they really are? To know where dual or multiple use of a given area is practicable and desirable, and where it is not, and to make actual and harmonious application of his knowledge?

Could those members of the Ecological Society who have to do with educational institutions make any larger or more practical contribution to the field than to work for the organization and inclusion in all college curricula of broad courses in ecology, and for the closer coordination of existing courses in different departments?

Our present practice, of turning out technical assistants who are ultra-specialists, is unfair both to the young graduates, to the community, and to the natural resources for which they may be responsible.

The program of this meeting of the Ecological Society bristles with information that shows what the ecological doctors are up against.

It appears that civilized man has taken Nature on a number of sprees, and the poor lady is a bit bedraggled. Note the obvious soil exhaustion as a result of wasteful cropping processes; soil erosion consequent on unintelligent practices or worse; decimation or even extermination of wildlife; overgrazing, not only on the vast open ranges of the West, but also, all too often, on pasture-lands in the East and South; wasteful logging and destructive burning of forests; plowing up of the native sod which should have been left for pasturage; exploiting our oil and other minerals; draining of marshlands for a prospective agriculture that can never be realized; reclamation of arid lands which can never pay the costs of development; importation of pests through careless introduction of foreign plants or animals; pollution of streams, lakes, and even the bays, harbours and shore waters of the open ocean with sewage and industrial wastes. Small wonder that Nature needs clinical treatment!

It is true that most of these unfortunate results have not been intentional. Some of the difficulties mentioned were probably inevitable in connection with the development of our agriculture and industry. But can we maintain our industries and our agriculture if we continue to waste our minerals, soils, water, vegetation and wildlife?

Up to now most of this process of exploitation and wastage has been little realized. From now on it should be recognized by all as inexcusable.

A first step in laying hold of an adequate remedy is diagnosis. Just what is wrong? And how can we cure the patient?

To a considerable degree we have begun almost feverishly to dope her with a number of different nostrums in advance of adequate diagnosis, until we have such unfortunate conflicts as the following: (Leopold, '34, p. 540). One road crew cutting a grade along a clay bank so as permanently to roil the trout stream which another crew was improving with dams and shelters; "the silvicultural crew felling the 'wolf trees' and border shrubbery needed for game food; the roadside-cleanup crew burning all the down oak fuel wood available to the fireplaces being built by the recreation ground crew; the planting crew setting pines all over the only open clover-patch available to the deer and partridges; the fireline crew burning up all the hollow snags on a wildlife refuge, or worse yet, felling the gnarled veterans which were about the only scenic thing along a 'scenic road.' In short," says Leopold, "the ecological and esthetic limitations of 'scientific' technology are revealed in all their nakedness."

"Such crossed wires are frequent," he writes further, "even in the CCC camps where crews were directed by brainy young technicians, many of them fresh from conservation schools, but each schooled in his particular 'specialty.'" Leopold emphasizes the unanticipated difficulties in securing harmonious land use, and maintains that "... to be a practitioner of conservation on a piece of land takes more brains, and a wider range of sympathy, forethought, and experience, than to be a specialized forester, game manager, range manager, or erosion expert in a college or a conservation bureau."

All present can doubtless duplicate or add to this rather sobering list of conflicts in the practical administration of conservation. One of the most spectacular was emphasized by J. N. Darling in a recent article. The Biological Survey was given \$8,500,000 for the reflooding of marshes and other measures for waterfowl and wildlife conservation. As Darling put it (Saturday Evening Post, September 21, 1935, p. 64): "... all the while we have been trying through the Biological Survey to *create* marshes, other agencies, other bureaus of Government have been spending vaster sums than we controlled to *dry up existing marshes* It is cold comfort to realize that they are doing this because they don't know any better."

No argument or sermon could be more eloquent of the need for integration, for synthesis, for the ecological approach, than some of these concrete

happenings in very recent times. Isn't it obvious that we do need a new Declaration of Interdependence?

Shall we continue to exert ourselves for conservation and rehabilitation of soil, while at the same time we permit an exploitation of the grazing range and allow cropping practices which make such recovery impossible?

Shall we erect huge dams for reclamation purposes, at large expense, and forget the watersheds above, denuded by overgrazing, with the result that silting up of the reservoirs and irrigation works proceeds at a rapid pace and may be counted on to utterly destroy the reservoirs in a few generations?

Shall we exert ourselves to set up natural areas and game refuges, to regulate hunting and to build up a favorable environment for big game, when the winter range of the animals is controlled by grazing interests that will not even consider the sale of their holdings to the Government, but insist on grazing the forage into the roots, to the ultimate destruction not only of forage plants, but also the soil, the big game, and even their own domestic livestock?

Nor can all the waste of natural resources be blamed on politics. Nobody will ever know how many millions of dollars in depletion of natural resources our ultra-specialization, our water-tight compartment type of teaching and research has cost us. Perhaps it is just as well we don't know. The total would be staggering. It is poor tribute to our scientific insight and small credit to our science. What can we do to popularize a broader, more truly ecologic point of view among ourselves and our scientific colleagues?

The ecologist should be able to look out on a piece of forest land or range land or farm land or into a stream, a pond or a lake and prescribe a regimen suitable for the total situation, each biotic community in its environment, a regimen which will take full account of all the special and local conditions and which will result in steady improvement of the whole.

Perhaps this is asking too much of one man. But is it unreasonable to require the ecologist at least to recognize the limitations in his information, so that he will make provision to fill the gaps in it when he becomes responsible for lands and resources administration?

Note that my objection is not to the production of specialists, but seemingly there is no valid reason why even a specialist should not try to see his problem as a whole.

Permit me briefly to run over some of the concrete problems in the United States of America, January 1936, to the solution of which, it seems to me, ecology has perhaps a larger contribution to make than has any other science.

I am purposely omitting discussion of theoretical or pure scientific aspects, although these are of fundamental importance. A conservation crisis, which means, doubtless, an economic crisis and a political crisis, continues upon us. The desirability of speed in adequate ecological application is so desperate

that I want to stress some of the current opportunities and responsibilities of the science in a number of fields.

Soil Erosion.—Bowman ('35a, p. 287) has pointed out that the protective sod has been ripped off much of the middle western region. Whole fields have taken flight. "In some places the ground has been literally blown off down to the plow sole." The dust storms, the erosion, the water shortage in so many localities, are in part traceable to a disturbed balance between vegetation and soils. Until recently nobody but a few ecologists seems to have realized the importance of *grassland*. The Committee on the Ecology of Grasslands of the National Research Council, made up of members of this Society, deserves encouragement. Bowman emphasizes the fact that it will take twenty or thirty years at least to begin to benefit from the tree planting in the shelter belt. In the meantime he asks how about working out a land use plan for the *grasslands* of the vast mid-continental area and starting to work it *now*?

Land Classification and Land Planning.—The land problems of the present National Administration (1935) are predominantly ecological. Who but a geo-bio-ecologist, one who knows something of interrelationships and of plant and animal indicators and soils, is qualified for the important tasks of land classification? Furthermore, will not his qualifications for the job be directly related to the richness of his experience, the comprehensiveness of his information and the breadth of his point of view?

A number of scientific articles in current periodicals purporting to discuss land problems disclose a painfully inadequate outlook. It happens that I am interested in wildlife. For the most part these articles either omit wildlife considerations altogether or dismiss them with a passing comment. This is unfortunate, for much of our submarginal land is probably more valuable for wildlife than for any other product of the soil. In fact a recent Government survey of soil productivity (Joerg, '35, p. 187) shows that no less than sixty-five per cent of the 1,903,000,000 acres of land in the United States, or 1,245,000,000 acres, is classed either as poor or non-arable. How about the wildlife possibilities of these lands?

The Natural Resources Board anticipates an increase in National population of from 15,000,000 to 17,000,000 people by 1960 (Joerg, '35, pp. 189–190). The Board apparently anticipates that to feed these people some 55,000,000 more acres of crop land will have to be provided. It is proposed to irrigate an additional 3,000,000 acres, drain 10,000,000 more acres, clear 10,000,000 additional acres now in stumps or trees, and plow 32,000,000 acres of present pasture land.

Have we learned enough to give an adequate inventory value to the *present* resources derivable from these lands: recreation, wildlife, water, forest, range, grass turf? Assuredly there should be no more reclamation, drainage, clearing or plowing without critical examination from the ecological point of view. We should avoid exchanging sure present values for problematic future ones.

Resettlement Projects and Subsistence Homesteads.—These projects, in ecological terms, are simply the exchange of impossible environments for others where it is hoped the settlers will have a chance. A nice job of ecological as well as economic appraisal of a complicated situation is called for.

Farm Sciences.—All the farm sciences, *e.g.* agronomy, horticulture, animal husbandry, plant pathology, veterinary science, economic entomology, etc., since they concern the relations between plants and animals and their environment have an important ecological aspect. This is true even of genetics!

Industrial and Engineering Enterprises.—"What the bio-engineer can do, no one yet knows," says Dorsey. We can quite easily see some of the things the engineer as we know him has done or has failed to do.

He has built a great material civilization but he has failed to properly dispose of the wastes of industry and the sewage from huge populations. Instead he has allowed these wastes to poison and contaminate our streams, lakes, estuaries, bays and even the open ocean, to the serious detriment of our enjoyment of nature, our health, and certain important natural resources. He has failed to provide for an appropriate social organization which will secure fair distribution of the beneficent products of his industries. By his narrow specialization he has brought the mechanical exploitation of a wide variety of natural resources, including human labor itself, to such a pass that the whole future of mankind is threatened.

Isn't it time that the important ecological aspects of these great industrial problems be given a little more adequate attention?

Conservation.—The layman applies certain "obvious" remedies to cure the ills of exploitation. In the wildlife field he reduces or closes the hunting season, cuts the bag limit, kills the hawks and owls. In the field of soils he puts in checkdams, launches huge programs of reseeding the ranges, weed control, rodent control. In the recreation field all too often he artificializes the environment, erects dams, "cleans" the water-courses, "improves" the streams, builds roads into areas that are immensely more valuable to an enlightened democratic people as wilderness areas than as landscaped tracts. But the obvious remedies often turn out to be no remedies at all. The ecologist, in the wildlife field, recognizes that reduction or closing of the hunting season may do little good without improvement of the environment; that indiscriminate killing of hawks and owls only makes things worse. In the field of soils management he realizes that checkdams, reseeding, and the various forms of weed and rodent control do very little good without correction of mistaken methods of land use, as for example, overgrazing on the arid western ranges, plowing and cropping of grasslands which should be reserved for grazing, or use for farming of areas which should be reserved for wildlife. In the recreation field the ecologist appreciates the fact that the natural environment is infinitely superior to any other as a valuable resource of all the people; that artificial environments are likely to defeat their recreational objective in proportion as they depart from the natural order.

Of all fields, none depends so definitely and inevitably on ecology as that of conservation of natural resources.

Aquiculture, Fisheries, Water Resources.—In his classic paper of 1887 Forbes pointed out that the organisms in a lake do not represent an accidental collocation of forms, but constitute an organized community. The oyster and fisheries specialist must take this into account. The plant-animal community in the stream, pond, lake, yes, in the ocean itself must be properly balanced and must have the proper environmental conditions if it is to afford a maximum quantity of beneficial product.

Reforestation, Range Rehabilitation.—Exploitation which has followed "mining" methods of forest use, with its attendant destruction of forest, forage, wildlife, and watershed values through over-cutting, land scarring, burning, and over-grazing has reduced millions of good acres to waste land. Similar "mining" has ruined a wide expanse of grazing land, and threatens a great deal more.

These gutted areas are now handed over to specialists for rehabilitation. The faith of some of the farmers and business men in science and scientific men is almost pathetic. Many seem to believe that various artificial measures, erosion control, reseeding, replanting, weed control, rodent control, or other measures will suffice to repair the obvious damage, even in the absence of removal of the over-heavy pressure from livestock which in the case of the grazing range is the fundamental and continuing cause of many of the difficulties. This procedure is like trying to cure a headache with headache powders and persisting in a round of night life. The stockmen themselves are slowly but surely coming to realize that unregulated competition for private profits and proper care of the land and its resources simply do not go together.

Formulas for the quickest repair of the damage done are now being sought by engineers in cooperation with ecologists. Who better than the ecologist, after all, can be counted on to see clearly through the processes which have been going on, to picture accurately the land as it ought to look, and to advise safely what should be done?

Wildlife Management.—Fundamentally wildlife management depends on a comprehensive knowledge of the environment and its potentialities for the production of plants and animals. The big problems are not propagation, introduction, control—they are rather restoration, soils, climate, food, shelter, proper utilization, maintenance of natural equilibria between plants, animals, and environment.

Medicine and Epidemiology.—The problems of the physician are often partly ecological. Many diseases are caused by biotic factors, protozoa, bacteria, parasites. Others depend on vectors, likewise biotic in character. Almost every ailment has a pronounced environmental phase.

Hippocrates, born over 400 years B.C., recognized that if a sufferer from tuberculosis remained indoors in congested districts he was likely to grow

worse, while if he spent his time out of doors in the hills he was likely to recover.

In a series of significant and interesting papers, Elton ('25, '29, '31, etc.) has examined the associations between causative organisms, their sometimes various carriers, and man. He concludes that ecology has a definite contribution to make to the epidemiology of mammals, as well as toward the solution of certain important problems in human disease.

Many of those here present must have heard Dr. Strong's address ('35) last June at the Minneapolis meeting of the American Association for the Advancement of Science, in which the importance of ecology in relation to disease received the chief emphasis.

Anthropology, Sociology, Economics, Ethics.—The environment impresses itself not only on the physical structure but on the mentality of peoples. Fashions, customs, even the mores, the fundamental life habits, are profoundly affected. Right and wrong are often functions of time and place. In a recent number of *ECOLOGY* Griffith Taylor ('34), in the determination of the movements of primitive men, assigns large importance to variations in climate and environment. The factors of food, climate and shelter he regards as all important. Other urges—seeking of adventure, making war, gaining of pearls or gold—hardly existed, he thinks.

What, after all, is more reasonable than the ecological approach to anthropology, economics, sociology and ethics? Man's evolution, development and behavior are inevitably so closely related to his environment that the ecological viewpoint seems the most natural in the world.

Education.—For man education represents perhaps the most important, potentially, of all environmental impacts.

How very far we are from making use of it for social betterment, for increased intelligence, greater welfare, and additional security! Why cannot we see the paradoxical and almost comical results of our tin-soldier regimentation of ideas and beliefs generation after generation! Graduating classes of large size each year—thousands of brilliant potential exponents of progress. And what happens? Each man and woman with rare exceptions goes forth and lives a life as stereotyped as the University President's phraseology in awarding each degree.

As Dorsey points out ('31, p. 901), "We expose children to a slightly modified course of Scholasticism and call it education; and because hundreds of thousands are exposed annually, popular education is supposed to follow."

My own son was interested in plants and animals until he took a course in science as a college freshman. One year was enough. The following year he majored in a field as far away from natural science as he could get.

We have the schools, says Dorsey ('31, p. 911), yet twenty-seven per cent of crime careers are said to begin at the age of fourteen or under; seventy-five per cent at the age of sixteen or under.

"Why should we have to keep a standing army of four hundred thousand men to guard our lives and property? Why should our robberies and homicides be so relatively more numerous than England's?"

"'Mental deficiency' they tell us; a psychologist's way of saying 'God's will.' Piffle! What are the facts of the juvenile courts? Seventy per cent of juvenile delinquents so normal mentally that there was no excuse at all to resort to that subterfuge. Removed from vicious surroundings and placed in a healthy environment, seventy per cent of children with both parents criminals were restored to society; eighty per cent restored where one or both parents were alcoholics; and eighty-one per cent where one or both parents were 'mentally defective' or otherwise abnormal."

Borderlands.—Dr. Isaiah Bowman, Chairman of the National Research Council, recently ('35*b*) has indicated "Borderlands in science and the training necessary for their cultivation" as one of five specific fields which the Council considers to be of major significance at this time. In further discussions of borderlands he points out that "The greatest borderland of all is that between the physical and natural sciences on the one hand and the social sciences on the other. It seems probable," says he, "that the cultivation of this great borderland will be the distinctive mark of the next epoch of advancement in organized research." Among all the sciences where can one be found with a more promising opportunity in this particular borderland than ecology?

Seemingly the hope of the future lies in the exploration of borderlands. Shall science, to paraphrase a recent writer (Joerg, '35, p. 205), while creating the machine and putting power into the hands of man, fail to teach him how to control the social consequences of the newly unleashed forces? This unfortunate and obvious threat to civilization can apparently be avoided only through an integration of the so-called natural and social sciences. The problem is one of borderlands, and to a very great degree ecological.

At this point a warning is perhaps in order. Ecology is no place for the traditionalist or the ambitious. "If you want to get elected to the National Academy," said a university president to the writer once, "select an old established science and stay right in the middle of it! Avoid, as a poison, getting out to the borders of your field!"

Richtmyer recognizes this entirely understandable prejudice against seeming innovation in his suggestion ('35, p. 380) that "... younger scientists not infrequently feel that they are 'losing caste' with their colleagues when they enter borderland fields. This attitude finds some justification in the fact that, until a given borderland field develops to the point of being generally recognized by administrative provision therefor, it is not easy for a young man entering such a field to secure a position."

Any strictures which may be felt by ecology and ecologists because of the borderland character of their field are more than made up for by the fas-

inating nature of the problems therein and the fact that the opportunities are unsurpassed for substantial contributions in both pure and applied science.

Nature is a great continuum. Borderlands exist only in the imagination of man. Why should one area in science be favored over others? Why should we neglect the so-called borderlands, most promising of potential sources of new and liberating discoveries and generalizations?

The National Research Council is doing a good job in stressing the need for breaking down "the watertight compartments that all too frequently are found in academic circles" (Richtmyer, '35, p. 382). The spirit of ecology is wholeheartedly behind this borderland program.

SUMMARY

1. Ecology is the science of all the relations of all organisms to all their environment.

2. There is great need for a "Declaration of Interdependence" between plants, animals, and their environment. These things are all parts of the same great unit system of matter and energy.

3. Harmonious and satisfactory land use and efficient conservation of natural resources can be obtained only through programs based on a sound ecological foundation.

4. If ecological instruction can be placed on a broader basis, and if ecological courses now offered can be properly coordinated, the contribution of the schools will be substantially strengthened.

5. The desirability of speed in ecological application becomes daily more pressing in our national and world conservation program.

6. Ecology is one of the most useful and essential of the sciences, in at least the following fields: soil conservation, land classification and planning, resettlement projects, all the farm sciences, certain industrial and engineering enterprises, aquiculture, fisheries management, practically all phases of conservation of natural resources, reforestation, range rehabilitation, wildlife management, medicine and epidemiology, anthropology and the social sciences.

7. As a science with an intense interest in so-called borderlands, seemingly ecology has opportunities and responsibilities second to none in helping to assure the basic essentials of a more abundant life.

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THE CRESCENTIC DUNES OF THE SALTON SEA AND THEIR RELATION TO THE VEGETATION

PETER J. REMPEL

University of Southern California, Los Angeles, California

The crescentic sand dunes, or barchans, near the Salton Sea, in the Colorado Desert of southern California, are mentioned, among other investigators, by MacDougal ('08), Free ('14), and Brown ('23), and more recently by Kniffen ('32) and Russell ('32). In most instances, the dunes are treated as a physiographic feature of the Salton Sea region, while in one account, that of Russell, some attention is given to their origin and formation. It seemed desirable, therefore, to determine something as to the ecological relationships existing between the dunes and the vegetation.

The investigation was begun on March 26, 1933. A station was established near Kane Springs, in Imperial County, at approximately $33^{\circ} 5' 35''$ N and $115^{\circ} 51' 15''$ E, where a four-cup standard anemometer and a wind vane were installed in order to determine wind velocities and direction. Stakes were set around six dunes of varying sizes, six stakes around each dune, three to windward and three to leeward. The stakes on the leeward side were forty feet from the edge of the leeward slope, one stake in front of each cusp and one between the two, all equidistant from the dune. The stakes on the windward side were all set at the very edge of the windward slope, one at either flank and one at the center of the arc formed by this slope. The distances from the stakes to the edges of the dunes were measured from time to time, and in this manner the direction and rapidity of advance as well as any changes in the ground-level outline of the dunes could be determined.

On February 5, 1934, the anemometer and wind vane were moved to a station located approximately eight miles north of Kane Springs. This location was considered more advantageous because of the situation near the northernmost dune in the field and directly in the path of the prevailing west wind, which has the greatest effect on the shifting sand; furthermore, the instruments were now directly between the source of the dune sand and the dunes themselves.

The area was visited at least once a month until June 4, 1934, instrumental readings being made by cooperative observers at intervals of one week at Kane Springs and daily at the later location. Due to unavoidable circumstances, several gaps appeared in the instrumental records, but the data obtained are sufficient to warrant certain definite conclusions.

THE DUNES

The barchans are situated on the west side of Salton Sea, on the gentle slope which lies between the sea level contour and the shore of this inland lake (245 ft. below sea level). The direction of slope is approximately from west to east. From about 5 miles north of Kane Springs the dune field extends northwards for 4.3 miles, varying in width from one-half to one and one-half miles. In this area, 120 to 130 barchans were counted. West of the dunes is the wide gap into the Borego embayment of the Colorado Desert.

The Substratum

Authorities agree that sand dunes take on the crescentic form most readily on a hard, level substratum. On the whole, this is true of the area here considered, of which the major portion is covered by a layer of coarse gravel and stones, a type of desert pavement produced by eolian deflation. The rock fragments of this layer are composed chiefly of sandstones, limestones, and compacted, calcareous clay-silt, with a scattering of quartzite, granite-gneiss, and basalt porphyry. The three sedimentary rocks are remnants of the bed of the ancient sea, or seas, which once occupied the Salton Sea drainage basin. The igneous and metamorphic rocks no doubt represent debris washed down from the mountains to the west. Further evidence of the old lake bed is found in the patchy occurrence of large broken slabs of the compacted, calcareous clay-silt, which are often encrusted by heavy deposits of tufa. The entire area is underlain by clayey soil, which becomes the surface soil near the Salton Sea.

On the whole, the dune area has a level surface. Some minor irregularities, such as low ridges and a number of shallow, dry washes, present but negligible obstacles to the advancing dunes.

Origin and Nature of the Sand Supply

Within a distance of eight or ten miles west and northwest of the barchans lies the beach line of ancient Lake Cahuilla, which in an earlier geological period more nearly filled the Salton Sink depression than does the modern Salton Sea. The old beach has become flattened with time and is now a broad belt of deep sand. This is the chief source of sand supply for the formation of the dunes.

The sand consists of well-rounded quartz grains with an admixture of a little feldspar and some rock fragments (Stuntz and Free, '11, p. 116). That a finer material with cementing qualities is also present is indicated by the formation of surface crusts on the dunes after rains.

Form and Size of the Dunes

As their name indicates, the dunes are crescent-shaped, with the hollow of the crescent facing to leeward of the prevailing winds (fig. 1). The small

proportion of dunes in this area that are not crescentic are either low mounds, smaller than the true barchans and in most cases preliminary forms of the crescent-shaped dunes, or they are large dunes with complex contours, resulting from the coalescence of two or more barchans, or possibly from modifications of single large barchans.

Since the windward slopes of the barchans are produced by drifting sand, they are long and gently rising, with a 7° to 12° slope; the leeward slopes, produced by the slipping or settling of the sand which is blown over the crest of the dune, are short and steep, with 30° to 32.5° slopes, the approximate angle of repose of the sand.

In a survey to determine the range in the size of dunes, eight barchans of various sizes were measured, all nearly perfect crescents. The smallest of these was 6 feet high at the crest of the lee slope; the windward slope was 80 feet long from foot to crest; the distance between cusp tips was 65 feet;



FIG. 1. Two barchans with a long cusp in foreground.

the depth of the arc formed by the lee slope was 8 feet. The largest measured dune was 63 feet high at the crest, the windward slope 220 feet long, with a distance of 450 feet between cusp tips, and a leeward arc 130 feet in depth. These measurements seem to indicate that there are certain changes in the proportions and outlines of the dunes along with increase in size. These changes will be discussed more fully under "The evolution of dunes," later in the paper.

Wind Direction and Velocity

Including the records from both stations, readings of wind direction were obtained for 200 days during the period from March 26, 1933, to June 5, 1934. Although the record is broken, numerous readings were taken during every month, and the daily record from February 5, 1934, to June 5, 1934, is complete. On the basis of the total record, the wind was from the west 46.4 per cent of the time. The percentage of winds from other directions ranged from the south wind with 10 per cent to the northeast wind with 3 per cent. On the basis of these records, augmented by the evidence

of the direction of dune movement and the unanimous testimony of the older inhabitants of this region, it may be concluded that the prevailing wind direction is from the west.

The records indicate also, that the highest wind velocities occur during the spring months, which is again borne out by dune movement and the observation of local inhabitants. On the basis of the complete daily records, February 5 to June 5, 1934, the following figures give some indication of wind velocities from various directions: the highest average velocity for a period of twenty-four hours, 30.3 miles per hour, was attained by the west wind, on May 1; average velocities for similar periods of winds from other directions were all below 12 miles per hour; the highest velocities of the west wind were recorded on May 1 and May 24, 40.3 and 46.1 miles per hour, respectively; average velocities for twenty-four hours of 10 miles per hour or more were recorded for twenty-five days out of a total of seventy-two for the west wind, and one day out of eleven for the east wind; at one time the west wind continued for fifteen consecutive days at an average velocity of 12.8 miles per hour; three days of south wind with an average velocity of 8.8 miles per hour was the nearest approach to this record.

The records for the fall months of 1933 are too incomplete to give reliable averages for that period. From the records at hand, however, it appears that the average wind velocities in the fall are considerably higher than those of the summer months, but lower than those of the spring months.

Winds with velocities of 5 miles per hour, or less, move little or no sand, and velocities of 15 or more miles per hour are necessary to move any considerable amounts; consequently, in the light of the figures given above, it is clear that the west wind is the only wind that can have any major influence on the dunes, and that this influence is least during the summer months. This west wind blows from the Borego embayment and is due, no doubt, to cold air drainage from the Pacific slope flowing through the passes of the Peninsular Mountains, which border the Colorado Desert on the west.

Evolution of the Dunes

Dune formation in general is described in the accounts of Cornish (1897), Cowles (1899), Stuntz and Free ('11), and others. King ('18), in his "Study of a Dune Belt," gives a lucid description of the manner in which barchans are formed on desert pavement. The wind tends to contour around a mound of sand instead of blowing straight over it, and since the drifting sand is densest near the surface of the ground, the sand advances more rapidly at the sides of the dunes than at the face, thus forming cusps pointed to leeward of the prevailing wind (fig. 1). The formation of small barchans at the cusps of large dunes was observed by the writer as described by King and also by Russell ('32, p. 116). Low mounds with gentle slopes are formed at the cusps of large barchans by the continued accumulation of sand which

is brought forward at either side of the dune. During a strong wind, small eddies with vertical axes move to leeward along the cusps, whirling up sand as they advance. When these eddies approach the tip of the cusp, they break and drop their load of sand, probably contributing materially to the growth of the low mounds. The mounds continue to grow until they are so high that the wind, whipping over the top, begins to eddy at the lee side. This eddy, whose axis is horizontal, results in the formation of a steep leeward slope. Because of the eddy, the direction of air movement along the ground-level to leeward of the mound is contrary to the direction of the prevailing wind; consequently, the movement of sand down the leeward slope is checked, and the steep lee slope typical of the barchans results. With continued growth, cusps are formed at either end of the lee slope, and the small barchan thus evolved begins to advance over the ground surface just like a large barchan, except that the rate of advance of the small dune is much more rapid, and the older barchan is soon left behind. The small eddies with the vertical axes, which appear at the cusps of the dunes, are probably produced at that point because it is there that the prevailing wind meets the backward sweep of the large eddy with the horizontal axis.

The evolution of the crescentic dune as observed by the writer differs in some respects from the evolution as described by King. According to that investigator's account, the change from the low dune to the barchan includes the following steps: a hump is formed at the highest point, the center, of the low mound; the hump moves forward from the center of the mound, with the greatest width of the mound correspondingly moved forward; a small, steep, lee face is formed on the leeward side of the hump, with the original, gentle lee slope forming an apron below the steep lee face of the hump; the steep slope continues to move forward until the apron below it is covered and the steep slope reaches the ground; and the cusps are formed..

As observed in the Salton Sea dune area, no humps were formed on the low mounds. The steep lee faces, no matter how small, were invariably found at the extreme leeward edge of the low mounds; consequently, the aprons mentioned by King were lacking (fig. 2).

Two notable changes occur in the dimensional proportions of a growing barchan. As the cusps are built up by sand drifting around the sides of the dune, the chord of the leeward arc becomes increasingly longer. In the same process, the windward slope becomes broader, presenting a wider and less rounded front to the prevailing wind. As a result proportionately more sand is carried up the windward slope than contours around the sides of the dune; consequently, the crest of the dune becomes higher, and the depth of the lee arc proportionately shallower. As the proportion of sand carried up the windward slope becomes greater, the degree of slope is increased, and, at the same time, the length of the slope from foot to crest becomes shorter relative to the other dune dimensions. The degree of slope on the leeward face remains approximately the same in all stages of barchan growth (table I).

In his discussion of the crescentic dunes of Peru, Douglass ('09) suggests that their shape is due to a double vortex of hot air which restores the scattered particles of sand to the center of the dune, and that the "broad wing" form of the Salton Sea dunes is caused by a reversal of vortices due to the rapidly falling temperatures at night. It seems improbable that this theory should be based on fact. As previously indicated, wind velocities of 10 to 15 miles per hour are necessary to transport considerable amounts of



FIG. 2. Leeward face of low mound, two feet high.

TABLE I. *Dimensions in feet of four crescentic dunes*

Dune No.	Height of lee slope	Length of windward slope	Pro- portions	Distance between cusp tips	Depth of lee arc	Pro- portions	Degree of windward slope	Degree of lee slope
1	6	80	1:13.3	65	8	8.1:1	7°	31°
2	13.5	160	1:11.8	165	35	4.7:1	9°	32.5°
3	20.6	100	1:4.8	125	32.6	3.8:1	10°	32°
4	63	220	1:3.5	450	130	3.4:1	12°	32°

sand in this area, and any upward or downward air movements caused by rapid temperature changes could scarcely attain such velocities; even if such air movements were possible, it is not clear how they would be instrumental in forming the broad barchans of the Salton Sea area.

Direction and Rapidity of Dune Movement

The direction in which the barchans advance is E 20° S, conforming with the direction of the prevailing wind. The line of advance may be temporarily deflected by inequalities in the surface of the ground or by cross-winds of sufficient velocity and duration. For example, stakes were set around a small dune which was advancing rapidly up the northwest slope of a low hill. While neighboring dunes did not vary in the direction of their advance, this

small dune shifted toward the northeast, *i.e.*, it swept around the shoulder of the hill. On one occasion the dunes were visited immediately after two days of fairly brisk north winds and several dunes were noted which had been shifted toward the south, one of the staked dunes having been moved eleven feet out of its course.

There are two major factors which determine the rate at which a dune advances, namely, the size of the dune and the wind velocity. The smaller the dune, the more rapid its advance, and the higher the velocity of the wind, the more rapid the advance. In a secondary manner, the influences which deflect the line of advance also influence the rate of advance. To illustrate, a comparison may be made in the rates of advance of a small and a large dune (table II).

TABLE II. *Rate of advance of a large and a small dune; dunes Nos. 1 and 4 of table I*

	Dune No. 1	Dune No. 4
Apr. 30-May 27	37.5 feet	17 feet
May 27-June 24	1 foot	no movement
June 24-Sept. 11	2 feet	1 foot
Sept. 11-Dec. 18	17 feet	4 feet

These figures afford also an indication of the differences in the rate of advance during the spring, summer, and fall seasons, conforming with the variations in wind velocities. The two examples just given probably approach the extremes in rates of advance. When the area was visited for the last time, on July 17, 1934, it was found that since February 24, 1933, a period of one year, four months and three weeks, dune No. 4 had advanced a total of 69 feet, while a small dune otherwise not included in the investigation had advanced a total of 133 feet.

THE VEGETATION

Lying within the Salton Sink, in the midst of the Colorado Desert, this area of crescentic dunes presents an extremely xeric plant habitat, and the vegetation is correspondingly sparse. The following list includes all the plant species encountered:¹

1. Perennial, evergreen, woody shrubs:

Larrea tridentata (DC.) Cov. var. *glutinosa* Jepson.

Franseria dumosa Gray.

Atriplex canescens James.

Eriogonum deserticola Wats.

Parosela emoryi (Gray) Hel.

¹ Plant species in general according to Jepson's "A Manual of the Flowering Plants of California. 1925"; species of *Oenothera* according to Phillip Munz, Pomona College, Claremont, California.

2. Perennial herbs—above-ground parts dead or dormant in summer:

Astragalus preussii Gray var. *limatus* Jepson.

Coldenia palmeri Gray.

Hesperocallis undulata Gray.

Orobanché cooperi (Gray) Hel. (Root parasite on *Franseria dumosa*.)

3. Annual herbs—appearing for a short time in the spring, and then only if precipitation is sufficient:

Cryptantha costata Bdg.

C. holoptera (Gray) Mcbr.

Dicorea canescens T. & G.

Geraea canescens T. & G.

Oenothera brevipes Gray.

O. clavaeformis T. & F.

O. decorticans H. & A. var. *condensata* Munz.

O. deltoides F. & M.

Psathyrotes ramosissima (Torr.) Gray.

Palafoxia linearis Lag.

Plantago insularis Eastw. var. *scariosa* Jepson.

Larrea tridentata var. *glutinosa*, the creosote bush, is the most numerous of the perennials, with *Franseria dumosa*, the burro weed, probably second in frequency of occurrence. Since the more sandy soils of the desert apparently afford the best habitat for the spring annuals, these plants are numerous here during a favorable spring, but during the spring of 1934 not one living annual was found, owing to the very meager precipitation.

Sand Blasting of Vegetation

In numerous instances, plants were noted which had been wounded by sand abrasion, and in every instance such wounding was restricted to the woody perennials. The injuries ranged from small wounds to complete decortication, and were invariably restricted to the west side of the stems, the windward side. Conclusive evidence that drifting sand rarely rises high above the surface of the ground is found in the fact that the injuries were most severe within the first two feet from the ground. An example of the decortication of *Atriplex canescens* is seen in fig. 3. Fresh wounds were not seen, and for this reason as well as the fact that the annual herbs, during their brief appearance, are entirely unaffected, it seems probable that sand blasting in this area is a slow process. No plants were seen which had been killed in this manner.

Vegetation Covered by Sand

Since most of the larger dunes are higher than the tallest of the woody shrubs, any plant in the path of the crest of a large advancing dune is in-

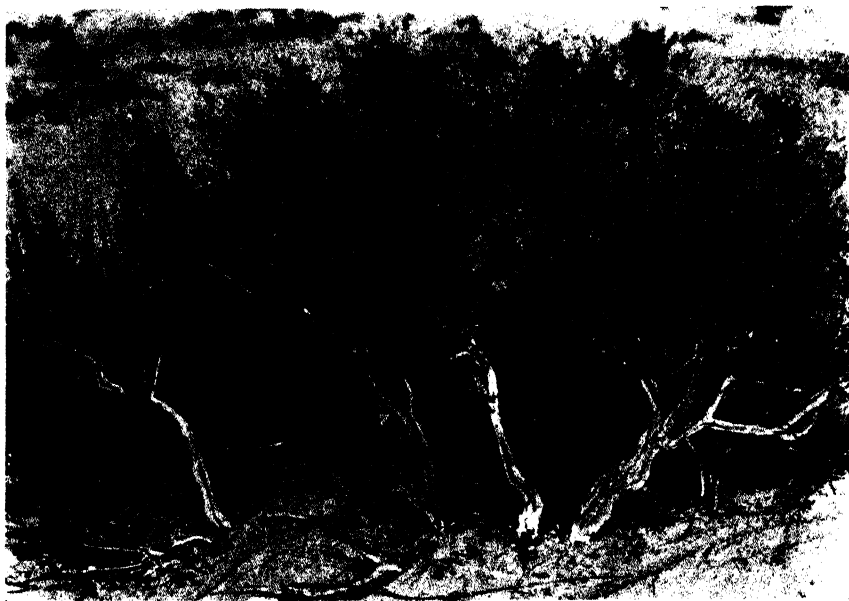


FIG. 3. *Atriplex canescens* decorticated by sand blasting.

variably overwhelmed and killed; the large dunes move slowly, and it may take years before the plant is uncovered again. Tall plants in the path of low dunes or the flanks of large dunes are defoliated below the level of the sand, but they usually survive. Low perennial shrubs may be completely covered by small dunes and uncovered again before they are killed. Dune No. 1 moved so rapidly that a low *Franseria* was covered and uncovered without harming the plant seriously. When this individual first emerged at the windward side of the dune, it appeared to be dead, but after a shower, which came soon afterwards, it recovered completely.

Very often vegetation is covered, or partially covered, by the drift sand which accumulates around the plants. By rapid elongation of their stems, apparently, certain species, particularly *Eriogonum deserticola* and to a lesser degree *Parosela emoryi*, keep their crowns above the surface of these sand accumulations and survive by this means. If the vegetation is closely grouped, the mounds grow until all but the tallest plants, and the species whose shoots elongate, are covered and killed. When this point is reached, there is no longer sufficient vegetation to bind the sand, and the mound is dissipated by the wind. The abnormally elongated plants are then blown over by the wind, and, with their leafy crowns lying on the ground, still rooted, still growing, form a striking feature of this area (see fig. 4).

Vegetation Belts

At the edges of the windward slopes and the sides of the barchans, the moisture brought by the late autumn and winter rains is protected against



FIG. 4. *Eriogonum deserticola* with elongated stems.

rapid evaporation by the thin layer of sand on the soil surface. This narrow strip forms a favorable seed bed, and in a short time a narrow belt of vigorously growing vegetation appears. These belts are especially conspicuous when the dune moves away in the spring and leaves a bare space between the dune and this belt of plants. *Eriogonum deserticola* appears to be a major constituent of such belts, and since this species has a thick crown of branches and leaves, sand continues to accumulate around the plants, and elongation of their shoots is particularly noticeable here. These belts often extend along the sides of the dunes as far as the cusps, and with the lateral extension of the dunes, which has been described, the flanks of the dunes encroach on the belts of vegetation. In some instances the elongating species survive even this deep layer of sand. An individual of *Parosela* which had been covered in this manner and left behind when the dune moved on, measured sixteen feet from the base of the crown to the surface of the ground. This was an extraordinary case, but elongations of three to four feet are common. Another feature of these two species is the phenomenal length of their lateral roots which extend through the dune sand. An attempt was made to dig out one of these roots, but it led into deep sand and broke off after thirty-two feet of it had been uncovered. It had no branch roots and was of nearly uniform thickness throughout. The crown of the plant from which this root originated, an individual of *Eriogonum*, was not more than two and one-half feet tall. Both species, growing under normal conditions, have short stems, rarely more than a few inches in length below the crown of branches.

The Vegetation an Agent in Dune Formation

Nearly all plants in the sand dune field have accumulations of sand to leeward, the size of the accumulations varying with the size of the plants

which form the obstructions. Where plants, particularly shrubs, are closely grouped, these small mounds coalesce to form larger mounds. These larger mounds again coalesce with others until a considerable area is covered by sand two or three feet deep.

Although the actual process was not observed, there was some evidence that such accumulations, when consisting of sand two or more feet deep, may be converted into barchans. As the depth of the sand increases, those plants which cannot elongate are killed and lose their capacity as sand binders. The large mound of sand is then free to shift and may take on the crescentic form. The following circumstance may be regarded as evidence in support of this theory. A small barchan was found about one hundred feet to leeward of an area which was denuded of all vegetation except a number of elongated individuals of *Eriogonum* and *Parosela*. There was no large barchan to windward of the small one; so it could not have originated in the usual way at the cusp of a large dune. Small dunes advance too rapidly and desert shrubs grow too slowly to allow for the elongation of the two species mentioned, if the dune had merely passed over the partially denuded area. It appears then, that the dune had originated and grown by slow accumulation in the area where the elongated plants were found.

Vegetation and Dune Stabilization

Chiefly for two reasons, it is impossible for vegetation to gain a foothold on the barchans. During the summer, the lack of moisture and the great heat prevent plant growth on the surface of the dunes, even though they are practically stationary for months at a time. During the balance of the year, when there is occasional precipitation, the wind velocities are highest, and the rapidly shifting sand prevents all plant growth.

Near the shore of the Salton Sea, several large mounds about fifty feet high composed chiefly of sand and clay were examined. They support a good growth of vegetation and seem to be permanently established, but they show no evidence of crescentic form, and their origin could not be determined.

SUMMARY

The crescentic dunes which lie west of the Salton Sea, on a substratum of desert pavement, obtain their sand chiefly from the ancient beach of Lake Calhuilla located to the west and northwest. The dunes are nearly all crescentic but vary greatly as to size and to a lesser extent as to proportions. The prevailing wind is from the west and attains its greatest velocities during the spring of the year. Wind has a direct influence on the formation of small barchans at the cusps of larger ones, and on certain changes in the proportions of dunes which take place with increase in size. Driven by the prevailing wind, the dunes advance across the plain in an easterly direc-

tion, the rapidity of advance depending on the size of the dune and the velocity of the wind; the smaller the dune and the higher the wind velocity, the more rapid the advance.

The sparse vegetation in the area is typical of true desert conditions. Plants in the dune field, particularly the woody perennials, often sustain severe injury due to sand blasting. The covering of the vegetation by sand brings about, variously, defoliation, death, or, in the rare exception of two species, a curious elongation which keeps the foliage crowns of the plants above the surface of the sand and usually results in their survival. Belts of vegetation are formed at the windward edges and sides of the barchans, where the thin layer of sand aids in the retention of soil moisture. Large mounds of sand are formed in areas where the plants are closely congregated, and it seems probable that these mounds may evolve into crescentic dunes. Because of the dry hot summers and the rapid shifting of the dunes during the balance of the year, the stabilization of barchans by vegetation is impossible.

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SOIL STRUCTURE AND SOIL BIOLOGY

ARTHUR PAUL JACOT

Appalachian Forest Experiment Station, Asheville, N. C.

INTRODUCTION

As Lars-Gunnar Romell has emphasized ('30, p. 842), "Burger ('22) with good reason, compares agricultural soil to an unorganized mass of building material, whereas the natural forest soil, with its definite, stable organization, is like a house built from this material." "It is more and more generally recognized that a natural soil, like a living organism, must be studied as a whole to get a correct idea of its responses" (Romell, '30, p. 843).

Romell ('35b) has indicated that most chemical analyses of soils have included a study of the chemical actions initiated by the sampling method which kills the organisms in the sample. Similarly most physical analyses may be compared to treating a block of brick buildings with dynamite, war tanks and steam rollers, before studying it, and then making a report that the structure was composed of so many per cent of 2" \times 4" \times 8" red units and so many per cent gray dust. The nearly amorphous mass would give no indication of the former floor space, rooms, capacity, or use of the building. Yet natural soil is as highly organized as a huge apartment house and as well tenanted.

All natural, shallow soil is a maze of tunnels and passageways averaging a millimeter in diameter, and harboring a varied and extensive population which keeps these channels open. The vertebrate animals (Taylor, '35), the larger insects (Blake, '26), the earthworms (Bornebush, '30, '32; Darwin, '81), the Protozoa (Cutler and Crump), and to a certain extent the Nematodes (Cobb, '14, '15) of the soil have been studied and their effect noted. The effect of Mollusca, which may not be important in the cold temperate zone, and the effect of the larger Myriapoda, which is important in mesic woodland, have been largely neglected. But of greatest importance, the work of the microarthropods, comprising the Pauropods, Scolopendrellids, Proturans, Collembolans, and free living mites, has been entirely overlooked, probably due to their size, intermediate between the macroscopic and microscopic, and to the need of special methods to find or obtain them. As they are slow, "play possum" on being disturbed, and are earth-colored, they are not noticed in a handfull of earth, although present by the dozens, as may be ascertained in part by examination of such material on a blue card under the dissecting microscope.

HISTORICAL REVIEW

In England, Cameron ('13, '25), Buckle ('21, '23), Morris ('20, '22, '27), and Thompson ('24) have found an extensive fauna of insects and larger

invertebrate animals in agricultural soil. In America, Shaler ('91) found that in a field near Cambridge, Mass., ants were so numerous that they moved enough material to cover the surface of the soil with one-fifth of an inch of new soil annually. This amounts to thirty tons per acre. Hayes and McColloch ('28) found thirty-seven species of Scarabeid beetles (including seventeen species of June beetles) in the soil of the vicinity of Manhattan, Kansas. Eighty per cent of these worked in plowed land, the remainder in sod or about old logs. In the same vicinity, Bryson ('31) found both beetles and bees burroughing in the soil, even to a depth of thirty-one inches, to pupate or hibernate, and to the extent of five to seven individuals per square foot. Later ('33) he found that 1760 pounds of soil had been excavated per acre by ants, bees and wasps on bare soil. Lindquist ('33) found that on Kansas prairie a species of Scarabeid beetle was responsible for two hundred burroughs per acre, burying twenty-one pounds of air-dried dung, and excavating one hundred twenty-six pounds of soil. Other species were also present. Their winter burroughs, dug in November, were twice as deep as the egg burroughs. Near Urbana, Ill., Weese ('25) found that in early October a large percentage of field insects migrated to adjacent woodlands to hibernate in the litter and underlying soil. Blake ('26) found that freezing and thawing does not kill or injure the litter and soil population, and that throughout the winter some of the species migrate up and down through the litter and soil to depths varying with the species or the intensity of the frost. Darwin ('81) found that earthworms in meadows and gardens moved a surprising amount of soil to the surface (seven to fourteen tons per acre annually) and that some species drew somewhat decayed leaves into their burroughs. This has been corroborated by Ramann ('11) and Bornebusch ('30, '32). Taylor ('35) reviews many examples of animals in relation to soil, but most of them are examples of extreme concentration, or of local interest.

These investigations bring out the fact that certain characteristic invertebrates of fields and meadows are annually mixing the soil layers and perforating them to a greater depth than the plow. It is significant that the nonvolant animals (earthworms) and the ants are the most important groups in moving soil vertically though dung-beetles attain a high degree of importance in cattle country. The work of mammals is local and, in woodlands, of cumulative effect only by centuries.

BIOTIC STRUCTURE OF OLD-FIELD SOIL

Perhaps the simplest soil with undisturbed structure is that of old or abandoned fields, say a field abandoned for four or five years and grown to tall weeds. In order to study the structure of such a niche a sample must be removed (with a kitchen knife) in such a way as not to destroy the structure by compression, torsion or shear. Such a block of soil an inch or two across, should be carefully placed top side up, on a rigid piece of card-board or

ply-board under a dissecting microscope with magnification of at least twelve diameters for examination.

Old field soil is most easily examined when rather moist, that is, when moisture is not evident as a film, but sufficient to cause adhesion of the soil particles. The surface of such soil (when seen under the dissecting microscope) is found to be littered with crumbs of organic matter, mostly bits of plants, finely broken up. This material is not available as food to most saprophytic animals until predigested by fungi. Scratching aside (with dissecting needles) this fine litter, or finding a bare spot, one is surprised to find a pavement of quartz granules or other minerals, the finer particles (dust) having been washed further down by the rain, leaving the coarser granules of pure mineral matter on top. It is on this micro-rockery that minute moss plants are dotted about often half buried among the crystals, and that filamentous algae trail their bright green threads. These two layers may be called the *rain drift layers*. Below the layer of coarse, well washed rock-detritus the soil is much darker and more varied in composition. It is the upper layer of fine litter, its floor of crushed stone and the soil just beneath it which harbors the highly colored and more active animals. Several species of spring-tails (blue, violet, and green) and mites, some of them vermilion and some green, and various insects, are to be expected.

The true soil appears granular, the various particles adhering in clusters separated by very irregular channels and passages. These passages are smooth walled where they widen to form chambers or causeways, thus much resembling the shaft to an ant's nest, except in direction. They are lined with pits and hollows like the surface of some meteorites, or of rocky streambeds with solution pits or pot-holes. These pits are sometimes formed on the under side or along the side of mineral granules (small bits of stone). The under face of such a stone fragment forming a cavern roof will glisten with moisture when the surrounding earth appears quite mat and only moist. Earthworm burrows differ in being much larger, direct (not meandering), and smoother walled. The clusters of solid earth between runways may be separated with a pair of dissecting needles. They are then found to be bound together by various types of rootlets, and by fungal hyphae which in some places become so dense as to have the appearance of a very loose felt. Moss roots are extremely fine, resembling fungal hyphae in their caliber. Grass roots are like a meshwork of gnarled ropes. The whole structure, when undisturbed and not deformed, is therefore much like that of some sponges.

In addition to the rootlets are to be found coarse bits of vegetation, like grass blades, bits of grass culm, bits of plant stalk, old rootlets and a surprisingly large number of grass seeds. A well decayed golden rod or *Erigeron* root-trunk under the microscope looks like the trunk of an old apple tree even to the knot hole where a lateral root once led off. Such a "trunk" may be hollow from end to end, forming a veritable vehicular tunnel. These vegetable tubes harbor masses of fine faeces left by the excavators. Faecal ma-

terial is considered quite a delicacy by the minute earthworms which will fill their digestive tracts with these predigested morsels. Elsewhere the root tube may be partially filled with much coarser, earthy faeces of much larger earthworms which have the habit of defecating in any underground hollows they may find (Darwin, '81).

The animal life to be found meandering about through this complex structure is astonishing. Volumes have already been written concerning the bacteria and protozoa, which are countless in numbers. Tardigrades (bear animalcules), though fairly common, are usually overlooked though they can be secured by means of the technique used to extract nematodes.

The most conspicuous life in such soil will be Collembola-like elongate Oribatid mites (*Ghn*). When exposed, these slender white animalcules scamper about seeking a lower, darker level. Their rather long anterior legs resemble antennae. They lack the transverse segmentation of the abdomen of the springtails (Collembola). Furthermore, the springtails have a roundish, flattened head with the antennae springing from its anterior margin. The springtails may be found along with the Oribatid mites and resemble them in actions. The most astounding phenomenon of such a quest is the perfect condition in which the animals are found when one would expect them to be more or less crushed or bruised. A more striking form is the bluish-white body of a *Japyx* or a *Scutigerella* weaving among the clusters of particles, its legs and antennae all aquiver as it moves along. Perhaps more numerous, especially in some soils, are the glassy nematodes which thrust their pointed ends into the crevices, their slender, firm, rounded bodies following without the titillating effort of the other forms. When disturbed they will curl into a Gordian knot. They evidently rest that way. Although most nematodes are difficult to see with a magnification of twelve, some individuals will be quite conspicuous, resembling a fresh, live rootlet.

A slender insect with quite long, antennae-like front legs reaching forward beyond its very small, narrow head, and a tapering vibrating yellowish abdomen, is the Proturan (or Yellow-tip), most primitive of insects. The immature forms are usually yellowish at both ends and white in the middle, or entirely whitish.

Under clumps of grass (even annuals) or weeds, will be found some small, white earthworms or pot-worms (Enchytraeids). Although so small as to be overlooked without a microscope they make up in numbers what they lack in size.

Tan, oblong animals with rounded corners, and eight prominent legs, the anterior pair of which is used for feeling, are predaceous mites (Parasitidae). Their pink mouth parts stand out prominently before them. They seem to be quite common under plant clumps along with the earthworms.

BIOTIC STRUCTURE OF HIGHER SOILS

Roots.—As vegetation becomes more dense, two factors are added to influence the soil, namely, an ever increasing layer of plant litter which more

and more eliminates the beating effect of the rain and its pavement of fine gravel, and an increasing complexity of roots. This root complex is of extreme importance in soil structure, for as the rootlets die, a process which is continuous even with perennials, fungi feed upon them and render them soft and punky. Then follow the saprophytic microarthropods which eat out this punk, usually leaving the bark as an indigestible, corky tube. In this way the soil becomes more and more pierced by a ramifying system of tubes. Time and trampling destroy some of them by crushing, and water percolation fills some with fine sediment, but many are left open, and more are being continually opened as new dead rootlets become available. The result of such channeling of the soil is to enormously increase percolation of rain water, aeration, and fertility, for the animals leave the empty rootlets lined with their droppings which, of course, are as potent as those of cows, both being based on vegetation and digested by "intestinal" bacteria, protozoa or both.

The depth to which such a fauna penetrates is probably equivalent to depth of root penetration. Road-cuts through woodland reveal black streaks and discs which, if carefully examined, are found to be made up of masses of minute animal faeces encircled or bounded by bits of root cortex. In fact it is easy to recover from woodland soils tubes of root cortex in the form of complete cylinders two or three inches long and varying from an eighth to three-quarters or more of an inch in diameter.

Anyone who has not cut into grass sod may examine figures of grass roots (Weaver, '19) in order to realize that the soil of grassland is most densely infiltrated by roots. Thus grassland soil is more copiously supplied with root channels and their included faeces, and is consequently more richly fertilized than woodland soils. Woodland soil, except when supporting a heavy growth of annuals or herbaceous perennials, is not well infiltrated with root-channels and their hair-lines of crushed faeces. Thus, woodlands poor in grasses and forbs tend to have soils more dense, compact and less organic, while grassland soils are friable and dark.

As to the numbers of microarthropods, it is a law of nature that increase in numbers is directly proportional to availability of food and protection. In the decayed rootlets protection is nearly one hundred per cent. Thus it may be stated that fauna is as abundant as local conditions allow, and that the numbers of individuals varies violently from one cubic inch to another, depending on the conditions of availability of food and of disturbance.

Faeces.—Mull soil is made up chiefly of worm castings and arthropod faeces. Where mull is rather fine grained it is derived from small worms (which are more numerous than large worms), where coarse (as in coves), from large worms. In some places the granules will be of two very different calibers, as if made by small earth-worms and larger. This can be ascertained without a hand lens. Another source of mull granules is the faeces of insects and other arthropods. Locally a mull soil may be made up of the faeces of millipedes (Romell, '35a). If the granular H-layer of some duff

soils be examined under a dissecting microscope it will be found to be made up in large part of oval and cylindrical bodies, black, grey or brown in color, which are the faeces of various insects. A great many of these faeces have fallen from the trees, bushes and other vegetation, to the extent of thousands per square foot. These faeces may be related back to the caterpillars (chiefly) or other insects which have produced them by studying the faeces of the caterpillars found overhead, since each family of caterpillar or insect has characteristic faeces.

Another source of the granular H-layer is the faeces of the animals which have chewed up the dead leaves of the L- and F-layers. The faeces from this source are very minute (a millimeter long or less) but far more numerous and dustlike. These black faeces are often found speckled and smeared about openings in dead wood and twigs in the litter.

Thus the H-layer is made up of three types of excrement, the coarsest from earthworms, the finest, chiefly from mites and springtails, the intermediate, from millipedes and from arboreal and epiphytic caterpillars and other phytophagous (and predaceous) insects, and small earthworms. Faeces of mammals, birds and the cold-blooded vertebrates are so scattered as to be accidental in square foot samples. Locally the excrement of millipedes (Romell, '35a), mollusca, and possibly rodents, form an important part of the litter.

As an example of the abundance of caterpillar faeces, I might give the following observation. On a University campus in North China the gravel walks were lined with fifteen year old *Sophora japonica* set some thirty feet apart. These trees were annually browsed upon by a Geometrid caterpillar, *Macaria elongaria* (a measuring worm much like the fall army worm), which, on certain trees (different from year to year) were so numerous as to completely defoliate the tree (thus causing it to set out a new crop of leaves). The faeces from these caterpillars formed semicircular, green, spongy carpets on the campus walks, one under each tree severely attacked. The next rainstorm would amalgamate this green rubble into a slimy green mat, deeper at the edge of the walk than in the center. Then the sun would come out and bake this sludge, with the liberation of certain characteristic (chiefly sour) gasses, into a rigid cake which would then crack and break up into pan cakes (the whole much resembling mud cracks). These cakes would gradually weather and abrade to dust and be blown about into the "grass" of the campus. In the woodland such a phenomenon is masked by the leaf litter and herbaceous cover, and though not usually of epidemic intensity, is nevertheless an important contribution to the H-layer each year.

I find no difference between the granular H-layer of some duff soils and of mull soil than that the mull is of a coarser nature, much deeper and of indefinite lower boundary.

ENVIRONMENTAL FACTORS IN THE SOIL

Soil Structure.—Under the microscope the soil resembles a jumble of rocks with the interspaces more or less filled with earth, that is, much finer particles. These rocks are coated with a film of water and organic matter (colloids). The ratio of rock particles (chiefly silica) to fine particles varies, but may be roughly divided into sand, loam and clay. Sandy soils tend to be drier and warmer, clays tend to be wetter, more compact and colder, while loams are a "happy medium."

Temperature.—The only effect of temperature outside of geographic distribution, is to inhibit activity and the reproductive cycle, for the saprophytic mites and probably all the microarthropods freeze and thaw as imposed by the temperature, resuming activity when thawed out.

Humidity.—The movement of the Oribatoid mites and probably all of the soil microarthropods is regulated chiefly by humidity. In brief it can be said that they ascend when humidity is high and descend when low or falling, some species being more sensitive than others. As sandy soils differ from loams and clays in moisture content one may expect a different population in these soil types or the population to be differently distributed.

However, the most striking difference in localization of species is to be found in soils which also contain different degrees of organic matter (and are therefore more constant in their humidity content). Thus mull soil (from the coves) harbors an entirely different combination of genera and species than do duff soils.

As the soil of a bare field becomes dry and baked the fauna moves deeper and deeper, keeping in that horizon where moisture conditions are suitable. Thus the vertical distribution of the population varies with degree of moisture, or depth of frost penetration (physiological dryness).

Aeration (ratio of oxygen to carbon dioxide) and pressure are of such minor importance, at least in the upper twelve inches as not to affect this population directly. The effect of *light* is felt only as it affects humidity, most of the species being eyeless.

QUANTITATIVE SAMPLES OF SOIL MICROARTHROPODS

Sampling Method.—Various methods have been used for extracting the arthropods (chiefly insects) from soil samples. All published methods are faulty in that the bulk of the microarthropods are not secured. The following two methods have proved most successful in making the faunal studies which form the basis of this report. This type of work was begun and carried on through various experimental stages, in semiarid north China. The work embodying the subjoined data was done as part of the Streamflow and Erosion project at the Appalachian Forest Experiment Station. I am indebted to the project leader, Dr. Charles R. Hursh for opening up this field to me in America and for valuable advice.

For heavy, clayey soils, a block about eight inches on a side is removed by digging around it carefully enough not to crush and spoil its internal structure. At the laboratory this rough block is pared down with a butcher knife to form a six inch cube. Thus it is advantageous to secure the block from soil as stone free as possible. This six inch block can then be cut into horizontal sections, preferably an inch thick. These sections are then placed on the sieves of the drying funnels, top side down. As the slabs dry out, the microfauna migrates downward along the channels and shafts which they have been using and maintaining. It is for this reason that it is essential

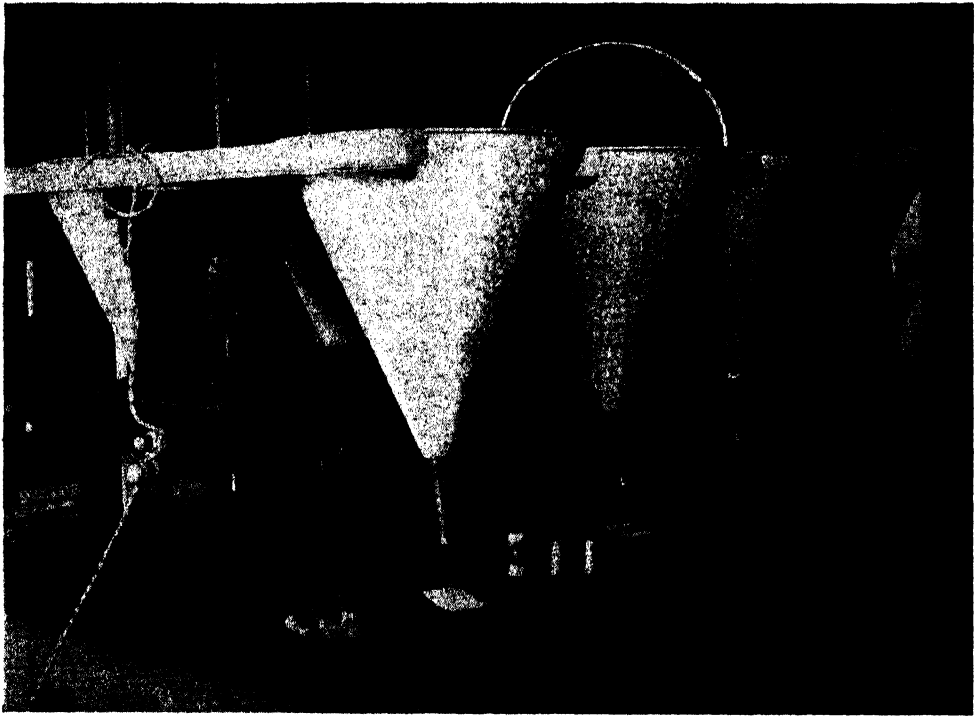


FIG. 1. Battery of drying funnels (B), showing main sieve (displaced) (A), sorting cones (C), and vial. The padding under the vials are cardboards used to hold the vial and cones close together. One person cannot attend to more than four per day.

not to destroy the structure of the block in removing it. In order to prevent the lower surface of the slab from drying out more rapidly than the interior of the slab and thus entrapping-by-desiccation slow-moving individuals in the center of the slab, a goose-neck lamp should be placed over the slab with a fifty watt bulb several inches above the slab.

For loams or sandy loams a set of galvanized iron collars eight inches in diameter and an inch high should be constructed, as well as a corresponding number of trays eight inches square with rims a quarter of an inch high turned up on three sides, the fourth side being sharpened. The sample should be taken a few hours after a rain, when the soil is quite moist but not wet.

To take the sample press one of the collars into the soil with the foot until flush. With a tray scrape soil away from one side of the collar then inserting the cutting edge of the tray under the lower edge of the collar, push the tray along lower edge of the collar until the entire collar rests on the tray. Label this sample "first inch." Press a second collar into the soil in the area thus vacated and with a second tray cut it loose as a sample of the second inch of soil. This may be repeated as deeply as desired. Each sample is taken to the laboratory in its container, a funnel sieve placed on its upper face, the sample thus enclosed flopped over, the tray removed, and the sample (still in its collar but on its sieve) placed in the funnel and treated as described in the preceding paragraph.

For friable, sandy soil, or soil which will not remain compact, the sample cannot be sprinkled on the sieves of the regular drying funnels because most of it would fall through. To circumvent this calamity a set of complimentary grills have been designed, such that, when superimposed, the bars of the upper grill cover over the slots in the lower (fig. 2). The two are placed in

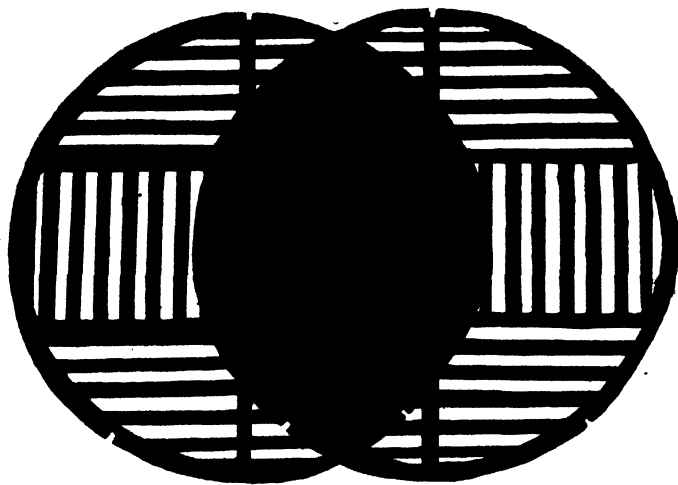


FIG. 2. Grills used for retaining sandy soil. Much reduced.

the mouth of one of two adjacent funnels, and oriented so as to form a solid floor. The sample is then sprinkled upon this floor to a depth of an eighth of an inch. By means of a string sling the top grill is then gently raised, and then lowered into the mouth of the other funnel. If the bars of the grills are slightly wider than the slots, any soil dislodged by the removal of the upper grill will be caught on this overlap. The grills at present in use have the bars half an inch wide and the slots three eighths inches, giving an overlap of one sixteenth inch each side. This is rather scant. The bars should be narrow enough to allow the minute animals to migrate off before they become too dry. The grills figured have but one drawback, namely,

that some of the bars are so long that some of the animals might travel the entire length of these bars before dropping off, and thus die of desiccation before reaching the edge. Thus a less continuous pattern would insure a more complete catch. Tempered masonite cut with a jig saw is fairly satisfactory material, though sixteen gauge brass cut on a nibbling machine is more satisfactory if the grill is not too large. The two grills must lie together perfectly flat to insure retention of all the soil particles.

The string sling used for raising the upper grill may be made of three strings of equal length tied together at one end. The free end is turned into a stout knot. The upper grill has three equidistant notches cut into the outer edge, each notch being the diameter of the string. The knot holds the string in the notch. A corresponding but wider notch should be cut in the lower grill to house the knot. As the total amount of soil held on the pair of grills is small, four or five sets are preferable.

A third device found particularly useful in sorting the catch, either soil or litter, but especially litter, is a combination of three cupped frustums the small end of which is formed of brass screening (fig. 3). The largest of

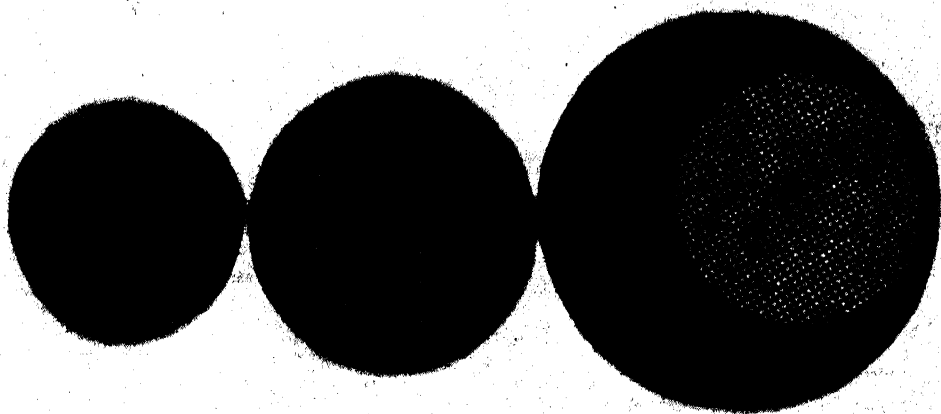


FIG. 3. Set of sorting frustums, showing relative sizes of screens (about natural size).

these frustum-sieves, cup about the lower end of the drying funnel. The sieves used are made of Tyler standard mesh, numbers 28, 48, and 80. These sieves retain the larger particles of soil and debris which fall through the drying funnel sieve, as well as the larger animals, especially the spiders. Thus the bulk of the fauna, which is made up of the smallest species, falls through into the vial, free from most of the debris, and not mixed with spider webbing, thus saving an enormous amount of time in sorting. The upper edge of each sieve should fit snugly against the shoulders of the sieve above it or some of the species will crawl up the sides of the sieve and squeeze out between them. For the same reason the receiving vial should also fit snugly

against the lower sieve. Thin copper is supple enough to make a snug fit. Thus the frustums should be made without projecting overlap.

In accordance with the latest sorting methods, the catch is spread on a glass plate (4" \times 5", photographic) to which is cemented a blue card ruled in columns the diameter of which is slightly narrower than that of the field of the microscope. A magnification of eighteen is sufficient for an experienced systematist, though twice that magnification is necessary for an inexperienced technician. The animals are removed with a number 0 paint brush moistened orally, and placed in a vial which must be kept agitated by tapping on the table to prevent some species from migrating out. The catch should be killed with a teaspoonful of boiling water or alcohol to cause the animals to die extended. If the vial under the drying funnel contains alcohol, the animals die contracted and consequently it is often impossible to identify them. In some cases it is easier to pick out the particles of debris than the animals.

Drying of material on the grills should be carried out without a heating unit which is lethal to thin skinned species. This air-drying process may take four days to two weeks depending on the humidity of the room atmosphere. An electric light (goose-neck) should be placed over the sample for the last day (or night) to drive down the most resistant species. Overhead lights should be left burning through the night to prevent nocturnal species from wandering up over the rim of the funnels, but the heat from these lights should be compensated by additional window ventilation (not draught). This process may draw minute insects from outdoors which may fall into the driers if the ceiling lights are over them. Such insects are usually quite foreign in aspect to the litter population though in some cases confusion may result. It is therefore highly advisable to shield the funnels from ceiling lights with muslin.

The above methods have been devised after several years of attempts with other methods. I do not feel however, that they are more than seventy to eighty per cent efficient. They are based on the fact that these microarthropods are particularly sensitive to desiccation and move downward with increasing dryness. By placing the samples upside down the animals may follow a short channel to the surface, whereas if placed top side up, the animal would have to dig its way through to the bottom, an exercise not always feasible, since only a few of the microarthropods are diggers. The greatest danger of loss of individuals is in causing their death by desiccation in the center of the sample. Any device for maintaining the moisture of the lower face of the sample until the remainder is thoroughly dried out would be an improvement.

Of the fifty species of Oribatoid mites found in the soil, only a small per cent have been accompanied by larvae and nymphs. As there are three nymphal stages and one larval stage for each species, this method fails to extract a considerable part of the population. Some of the immature forms

are unable to travel (Phthiracaridae) while others are imprisoned in the rootlets or plant parts and the collecting method is unable to extricate them.

Thus the statistics given below are merely an indication of the total fauna of the samples and should not by any means be regarded as a total catch. Finally, in all this work it is necessary always to remember that the method used sorts out species of certain tropisms and habits while species of different or contrary reactions are not secured. I do not regard the total number of individuals per unit volume of much importance, though interesting. Far more important is the relative numbers of the individuals of each species. This however, is of use chiefly as an indication of the probable value of determining the *function* of that species.

Samples Taken.—All lots were taken from, or near the vicinity of the Bent Creek Experimental Forest, ten miles southwest of Asheville, N. C.

TABLE I. "Saprophytic" Mites from soil samples

Kind	Lot Age Area Depth	F19 4 yr. 50 0-2	F29 4 50 0-3	F20 4 50 0-2	F27 4 50 0-2	F13a 45 120 1-2	F23.2 12 36 1-4	F32 45 30 11-13	F21 80 92 1-3	F21r 80 — 4	F22.1 80 36 1-4	F22.2 80 36 4-7	F30 30 64 10-13
<i>Tectocephus velatus</i> (Mich.)		14	5	154	4	178	5	1	11	2	6	2	
<i>Oppia corrugata</i> (Berl.)		1	2	14	5	66	4		587	26	5	7	5
<i>Epilohmannia minuta</i> Berl.		16	3	30	11	85	1		6		1	2	3
<i>Oppia sml.</i>		3	5		25	11	18		40	1	7	3	5
<i>Xylobates oblonga</i> rbt.				8	1		1		60	2	2	1	
Ghn.						1	27	1	1	6	205	4	
<i>Suctobelba lxn.</i>			2		3	15	6		10		1		
<i>Trhypochthonius americanus</i> (Ew.)					2	3	1		8		1	1	
<i>Eremulus pct.</i>				24	36		13				1	5	
<i>Eremobelba lpd.</i>				2	4		3		3		3		
<i>Pseudotritia ardua</i> (Koch)				1	2	26			2		1		
<i>Cultirribula confinis</i>													
Berl.		10	1		2		8		4				
<i>Xylobates ngt.</i>			1	13	13	17		1					
<i>Monieziella trn.</i>			8				3	4	10				
<i>Oppia fls.</i>				3		21	6	1					
<i>Ceratozetes subaquila</i> mnr.									509	41	8	3	
<i>Malaconothrus.</i>										1			
<i>Oppia nst.</i>				6					29	4			
<i>Suctobelba frm.</i>						14			3			1	
<i>Nanhermannia dorsalis</i> (Bks.)								1	34		1		
<i>Rostrozetes ppl.</i>							1		7	1			
<i>Oppia brt.</i>				4	9		2						
<i>Malaconothrus mrn.</i>						5	5	1	4	3	1	1	
<i>Lohmannia fls.</i>						3	1	2					
Pld.									8	10	2		
<i>Carabodes flt.</i>									38	4	1		
<i>Microzetes ppl.</i>				2	3								
<i>Brachychthonius crt.</i>		23				8							
<i>Suctobelba hrh.</i>						74	10						
<i>Suctobelba pnt.</i>						3	5						

TABLE I. *Continued*

Kind	Lot Age Area Depth ..	F19 4 yr. 50 0-2	F29 4 50 0-3	F20 4 50 0-2	F27 4 50 0-2	F13a 45 120 1-2	F23.2 12 36 1-4	F32 45 30 11-13	F21 80 92 1-3	F21r 80 — 4	F22.1 80 36 1-4	F22.2 80 36 4-7	F30 30 64 10-13
<i>Brachychthonius ber- leseii</i> Wlmn.....			2			3							
<i>Galumna curvum</i> (Ew.)		2	1										
<i>Peloptulus americanus</i> (Ew.).....					2	2							
<i>Suctobelba srr</i>							2		2				
<i>Zetes trn</i>								1					1
<i>Scheloribates lanceo- liger</i> Berl.....									96		1		
<i>Ceratozetes subaquila</i> lhn.....									55	1			
<i>Liacarus</i> spg.....									33		1		
<i>Eremobelba pct</i>									5	2			
<i>Oppia</i> fld.....											1	3	
Mln.....											1	2	
<i>Hypochthonius rufulus</i> (Herm.).....											1	1	
<i>Oppia</i> lvs.....					91								
<i>Eremulus</i> cnt.....				7									
<i>Nothrus terminalis</i> crn.					5								
<i>Oppia</i> spl.....				4									
<i>Brachychthonius</i> sms..	3												
<i>Pelops bifurcatus</i> Ew..						3							
<i>Oripoda?</i>			2										
<i>Nothrus</i> slc.....									7				
<i>Eremaeus oblongus</i> Koch.....									5				
<i>Suctobelba</i> frg.....									5				
<i>Camisia segnis</i> (Herm.).....									4				
& 18 spp.....						1	2		15	3	1		
Total Number Species		8	11	14	17	20	22	9	40	16	22	14	4
Total Number Individuals.....		72	32	272	218	539	124	13	1601	106	252	36	14

Lot 34F19. Fifty square inches (1/3 square foot) from tall-weed old-field, from top of a low swell; had been planted to white pines, cut, the litter burned, and planted to corn, then abandoned four years; included a small leguminous plant, a little moss and debris, thus constituting a representative sample; to two inches deep; taken November 26, 1934.

Lot 34F29. As preceding but including part of a daisy clump; to three inches deep; taken April 5, 1935.

Lot 34F20. Fifty square inches from tall-weed old-field; abandoned four years; from semi-weedy spot; to two inches deep; four or five miles from preceding; taken December 15, 1934.

Lot 34F27. As preceding but from a fourteen degree slope, three hundred yards further; to two inches deep; no perennials; taken March 21, 1935.

Lot 34F13a. One hundred twenty square inches (six-sevenths of a square foot) of sod soil (plants shaved off and surface scraped clean); to

one and a half inches deep; from top of a low swell in closely browsed *Andropogon* pasture forty-five years old; taken October 23, 1934.

Lot 34F23.2. Six inch square block from a depth of one to four inches deep (top inch removed), old-field, *Andropogon* cover; abandoned twelve years; unbrowsed, untrampled; taken February 6, 1935.

Lot 34F32. Thirty square inches, between eleven and thirteen inches in depth, brown loam with fragments of schist, badly shattered block, from an *Andropogon* bald on an isolated knoll 650 feet above the French Broad; abandoned forty-five years; taken April 17, 1935.

Lot 34F21. Ninety-two square inches taken from surface of mineral soil down two to three inches (thus including a sprinkling of the H-layer); from eighty year old pine-oak woodland; taken January 7, 1935.

Lot 34F21r. From green root one inch by six inches, including a lateral eight inches long with its adherent earth (about one and a half ounces) same spot as preceding, four inches deep, same date.

Lot 34F22.1. Six inch square, one to four inches deep (top inch removed, thus no trace of blackish organic soil), brown soil, same locality as preceding, two yards distant; taken January 30, 1935.

Lot 34F22.2. Six inch square, four to seven inches deep, immediately below preceding, red clayey soil; same date.

Lot 34F30. Eight inch square, ten to thirteen inches deep, red clay with disintegrating pieces of mica schist, under thirty year old pine-oak woodland (old-field), formerly *Rhus-Robinia*; taken April 15, 1935.

Lot 34F33.1. Nine inch square, upper four inches of *mull* soil, including many roots and rootlets, cove, northern exposure, steep slope, southern hardwood cover, no brush, few forbs; taken April 25, 1935.

All the above blocks were dried *in toto*. The *mull* sample was not exhausted until a month had elapsed (room humidity). Other samples were exhausted in from one to two weeks.

Census of Fauna Recovered.—As already indicated, the sampling was done in such a crude way (drying blocks two to four inches thick *in toto*) that the results must be regarded as constituting only a part of the entire population of the unit sampled.

Only the saprophytic mites (Oribatoidea and Tyroglyphoidea) have been determined to species. As many of them are undescribed or the descriptions are in press or with editors, a symbol has been used to designate them. As the symbol comprises the first two and the last consonants of the root of the specific or generic name, it will be an easy matter to relate each symbol to the complete name, once it is published. For instance lb = *alba*, ngr = *niger*, fsc = *fusca*, and so on. In view of the extensive and immediate interest in soil conservation and land use and the direct application of the data recorded in this report, it is deemed best to use this method rather than to delay publication for two or three years before all the specific descriptions have been published.

In comparing these samples, it should be borne in mind that lots 34F19, -20, -27, and -29 (fields abandoned four years) include a thin sprinkling of weeds. In order to gain space in the columns the initial 34 is dropped from the lot numbers. The numeral under the lot number indicates the age of the vegetative covering which developed after the last plowing, the next one below that indicates the area in square inches of the upper face of the sample, while the lowest indicates the depth of the sample in inches. The lots to the left of the double line are from unwooded land, those to the right are from wooded.

TABLE II. *Census of Arthropods.*

Lot.....	F19	F29	F20	F27	F13a	F23.2	F32	F21	F21r	F22.1	F22.2	F30
Age.....	4 yr.	4	4	4	45	12	45	80	80	80	80	30
Area.....	50	50	50	50	120	36	30	92	—	36	36	64
Depth ..	0-2	0-3	0-2	0-2	1-2	1-4	11-13	1-3	4	1-4	4-7	10-13
<i>"Saprophytic"</i>												
Saprophytic Mites..	72	32	272	218	539	124	13	1601	106	252	36	14
Spring-tails.....	163	586	133	56	104	56	8	270	40	36	7	7
Larvae.....	?	2	?	—	12	2	1	4	3	—	—	—
Proturans.....	—	2	—	—	—	1	2	9	2	1	1	1
Millipedes.....	—	5	—	—	—	3	10	22	2	—	—	3
<i>Predators</i>												
Mites.....	199	278	85	50	144	73	27	260	77	50	4	20
Ants.....	—	114	—	—	41	151	—	2	—	—	—	14
Beetles (ad. and im.)	—	14	—	1	10	6	—	9	—	—	2	—
Centipedes.....	—	2	—	1	3	4	1	5	—	3	—	—
<i>Vegetarian</i>												
Hemiptera.....	—	10	—	—	84	4	—	7	1	1	1	—
Thrips.....	—	3	—	—	15	2	—	3	—	—	—	—
Total Individuals...	434+	1048	490+	327	952	426	63	2194	161	343	51	59
Total Individuals per sq. ft.....	1300+	3024	1470+	936	1140	1804	303	3434	—	1372	204	133
Total per sq. meter = 10.764 times the number per sq. ft.												

Under predaceous mites are included Pediculoid, Scutacaroid and hypopial nymphs of Tyroglyphoid mites.

As lots F19 and F20 were originally in the nature of preliminary tests, the insects and myriapoda were not listed.

TABLE III. *Soil Population per Square Foot*

Soil depth	No. saprophytic mites	No. saprophytic insects and myriapods
1"-3"	2800	500
2"-4"	1320	148
5"-7"	340	32
10"-13"	28	22

From the three tables six facts are obvious: (1) microarthropods are abundantly distributed throughout natural, vegetated, mineral soil to a depth of at least a foot, (2) the numbers of any one species fluctuate widely from lot to lot (depending on the local abundance of food), (3) the number of species and individuals diminishes with soil depth (from 1800 at one to two inch depth to 130 at ten to thirteen inch depth per square foot of surface, in a partial catch), (4) these animals arranged according to diminishing abundance are Oribatid mites, other mites, spring-tails, ants (chiefly one species), hemiptera (chiefly one species), myriapods, thrips, beetles, miscellaneous, (5) soil of old, mesic grassland has the most abundant fauna, (6) although the soils of various culture types harbor about twenty species of saprophytic mites, these species differ in the different culture types.

The lower layers (five inches to seven inches and ten to thirteen inches) contain the same species as are found in the upper layers (with one exception). Some of these species and genera are not found outside the soil proper, except by accident. The largest number of different species occur in the upper inch, especially in the H-layer although it is only a few millimeters in thickness. From a depth of two inches downward a total of twenty-two species of saprophytic mites were recovered. Some of these soil species are litter species which have entered the soil to lay their eggs. Litter species which lay their eggs in the mineral soil are not eliminated by woodland fires.

Only one sample (9" × 9" × 4") of mull soil was obtained (lot 34F33). Of the seventy species (870 individuals) of saprophytic mites which it yielded, only twenty-five were found in the duff and old-field soils. Of the forty-five species found only in the mull soil sample, sixteen were represented by one individual only, probably having been jarred out of the litter when removed. Of the twenty-three species found only in the duff soil samples, seven were represented by but one individual. Discarding species represented by a single specimen, we have twenty-nine species which seem to be typical of mull soil and sixteen species of duff soils. In brief the saprophytic mite fauna of the mull and duff mineral soils (A₁ layer), is radically different. This difference is undoubtedly due to the additional factor in mull soils of greater amount of organic matter and of moisture. Many of these soil species may be found in the litter under certain conditions.

FAUNAL NOTES

Earthworms are not microarthropods, but the following notes are not out of place here. These animals dry out *in situ* or on the sides of the funnels to which they adhere after falling through the sieve. If they reach the receptacles they are all shriveled up and undeterminable. Thus this method of collecting is not suited to a study of the earthworm population. In the area under consideration an abundance of minute species, possibly Enchytraeids, were recovered from old-field soils especially about such perennials as daisies

(*Chrysanthemum*). A good deal of soil of old-field woodland is populated by small Lumbricids which are so small as to be usually overlooked and the sample recorded as without earthworms. Mull soils (in the coves) are tenanted by the larger species. Earthworms are of cardinal importance in maintaining soil channels and a good mixture between the H-layer and the mineral soil. A quantitative survey of the earthworm population of different types of soil under different kinds of cover is much needed over all of the United States. Species of *Bimastus* are characteristic of forest litter as well as *Octolasion lacteum* and *Lumbricus rubellus* (Olson, '28).

Mites.—The predaceous species were not determined. In one tall weed field (34F19 and 34F29) two or three species of *Pygmephorus* were abundant and therefore give a very high number of "predaceous" mites for those lots. I do not think this genus has any direct relation to soil structure. Although I am quite certain that perhaps as much as one half of the Oribatoidea are not saprophytic, since they are usually so regarded, I am referring to all of them, as well as the Tyroglyphoid *Monieziella trn.*, as saprophytic mites. Some of them are directly concerned in channeling the soil and they are far more numerous per unit area than any of the other groups of segmented animals. Adults are small enough to eat out rootlets one-tenth millimeter in diameter. Their function is feeding on the fungi, the trituration of fungus softened dead roots and rootlets, and the reduction of this material through the action of the flora and fauna of their digestive tracts. Their form is characteristic of soil animals, namely, somewhat elongate, but stout, with no midthoracic constriction, with blunt ends, legs, especially tarsi I and II short, more or less armed with spines which are usually short and stout. Such mites are *Lohmannia*, *Epilohmannia*, *Xylobates*, *Malaconothrus*, and such Tyroglyphoids as *Rhizoglyphus* and *Monieziella*. These forms are truly fitted for digging and should be distinguished from many other soil mites belonging to other genera which are not morphologically specialized for digging but are found exclusively in the soil. They may be fungus eaters.

In the above list of mites recovered from soil, most of those in lot 34F21 were undoubtedly present in the very thin (2–3 mm. deep) H-layer and therefore not an element of the soil proper. It is impossible to remove the fauna of the H-layer without removing part of the A₁-layer. In practice therefore, where there is a covering of organic litter, the upper half inch of mineral soil should be removed or sterilized before making an analysis of the soil fauna. Moreover, in taking a forest soil sample every precaution should be taken to prevent mites from falling onto the sample from overhanging trees or from being snapped onto the sample from nearby vegetation. Any dead leaf or twig may contain these mites. Species represented by a single individual may be regarded as accidental.

Some mites regularly found in the soil of one area which may be rather dry, with little litter covering, may be regular denizens of leaf litter in a more moist area with abundance of leaf litter. This is due to the tendency of these

mites to occupy layers of certain degrees of moisture rather than to be influenced by temperature, structure, or kind of organic debris. Certain mites will not be found in pine litter, not necessarily because of any difference in the food value of pine leaves compared to oak or maple, but because some pine leaf litters are drier than deciduous. These absent mites might, however, be expected in the H- or A₁-layers of the same pine woods. In brief, Oribatoid mites orient themselves vertically according to the moisture of their medium. Thus no mite is confined to any one soil depth (unless depth is measured in meters).

Collembola are the second most numerous group of microarthropods. Although not fitted for digging they undoubtedly are important in keeping open the channels formed by the mites. Most of the soil species are eyeless and unpigmented (white). Some of these species feed on decayed vegetation and are therefore important in opening up new soil channels.

Ants are the most active of soil animals. Every square yard of vegetated, mesic soil harbors at least one colony of ants. Some of the species are *very minute* and yellow so that they may be easily overlooked. In the area studied several *Ponera coarctata pennsylvanica* or *Myrmecina graminicola brevispinosa* or both are present in every square foot of litter, while the minute yellow *Brachymyrmex heeri depilis* or *Solenopsis pergandei* are seldom absent from square foot soil samples (an original series was determined by Professor Wheeler). The funnel method of sampling reveals their presence but they will easily escape if there is no cover over the top of the funnel or if the sorting sieves do not fit snugly together. Not only do the ants dig their own shafts but they maintain ramifying chambers. Some ants store weed seeds. A quantitative study of ant populations in different types of soil under different vegetative covers is much needed over the United States.

Myriapoda.—Micromyriapods (Pauropoda and Scutigerellids) constitute the bulk of soil myriapods, at least during the warm, moist season. Young of the larger species are also common locally. Millipedes are a woodland group and demand a certain degree of moisture. Much more attention should be given to the effect of millipedes on soil.

Miscellaneous insects.—Pink mealy-bugs are common in most soils. Proturans though typical of the litter are also found in the soil, usually as immature forms. Thrips, Staphylinid and Pselaphid beetles are usually found in every square foot. *Japyx* may occasionally be found. All these insects though not feeders on decayed plant parts are continually using the channels and thus helping to maintain them.

The soil fauna comprises the following definite *functional* elements:

Residents

- Saprophytic (eating dead vegetation).
- Fungivorous (eating molds and mildews).
- Coprophagous (eating faeces).

Necrophagous (eating dead bodies).

Predaceous (catching and eating living animals).

Phytophagous (eating or sucking living plants—chiefly roots; or if leaves then at night, harboring in soil during heat of day; seeds (as ants).

Nidicolous (inhabiting nests of other animals as moles, ants, etc.)

Nonresidents

Nidifacious (making nests in which to lay their eggs, but feeding elsewhere).

Pupating in soil (as certain caterpillars).

Parasites (laying in wait for their host).

Seasonal (passing the winter in hibernation or a dry season in aestivation).

Although all these groups of species may be instrumental in forming or maintaining (or both) channels through the soil, only the first group is of interest in eating out dead roots. The last group is very important in maintaining soil channeling through the winter as described by Blake ('26). This is particularly important in the warm temperate zone where the snow cover is intermittent.

GENERAL CONSIDERATIONS

Microarthropods are abundantly distributed throughout natural, vegetated soil to a depth of at least a foot. This *animate layer* varies in population with development of roots and rootlets. The lower limit of this layer is therefore indefinite, fraying out below as does the root layer. Soil erosion eliminates this porous, channeled layer with its makers. Resowing of this fauna is useless without precedence of a vegetative covering. Under natural conditions repopulation of abandoned agricultural land by the dead root eaters is very slow, unless they can be washed down from a higher slope. Artificial restocking of rewooded agricultural land would therefore be highly advisable to rapidly improve soil tilth and soil fertility. Furthermore, if the forester wishes to develop a dark, friable soil where there is normally a compact yellowish or brownish soil, it will be necessary to encourage the growth of a dense herbaceous carpet, preferably grasses.

As many of these species are *confined* to the soil as a medium, spending their entire lives in the soil, they are more characteristic of the soil than so called soil insects which, for the most part, pass at least one stage of their lives above ground. I would therefore adopt the definition of a soil fauna or of soil animals, as those animals which normally spend all of their lives in the soil (geobionts). This includes the moles, possibly the shrews, the glass-snake (*Ophisaurus ventralis*), certain amphibia in wet soil, possibly the mole cricket, certain Thysanura and Proturans, more Collembola, still more mites, certain earthworms and pot-worms (Enchytraeids), certain Nematodes, certain Tardigrades, and some Protozoa. Those animals which spend part of their lives in the soil either as egg or immature stage, or as adults (for hiber-

nation, aestivation or oviposition) I would refer to as soil transients (geophiles). Strays are geoxenes. Furthermore I would divide the soil fauna into two categories; the basic, including those species which are directly responsible for certain phases of soil structure and soil changes as earthworms, burrowing Oribatoidea, and eaters of dead roots, and the secondary, including micropredators, parasites, and other forms which do not directly cause soil modifications. This would place moles, shrews, and mole-cricket among the basic soil animals, for although predaceous they are positive factors in influencing soil structure, even though in a limited way or only locally.

In all evaluation of soil animals one should draw a sharp distinction between animals which affect the soil locally, however intensively, as prairie dogs, and those which are of general occurrence (in all vegetated soils). Much of Taylor's ('35) article is concerned with species of local importance only. Such data are not of general interest or applicability. It is the ever-present, generally distributed faunal elements like the Oribatid mites, minute earthworms, spring-tails, and ants which are of cardinal, general interest in soil improvement. They make up in numbers what they lack in size.

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THE VEGETATION OF THE KATMAI DISTRICT¹

ROBERT F. GRIGGS

The George Washington University, Washington, D. C.

Endeavoring to gain some idea of the vegetation of the Aleutian region before my first departure for Alaska in 1913 and finding nothing satisfactory in the literature I naturally resolved to supply the deficiency. But in the field I found it impossible to describe the vegetation in terms and concepts borrowed from the ecology of temperate vegetation. This experience was repeated on five subsequent visits to Alaska, 1915-1930, as leader of the National Geographic Society's Katmai Expeditions² which meanwhile discovered and explored the Valley of Ten Thousand Smokes and the adjoining country. Not until it was realized that arctic ecology must be approached from an entirely different point of view than that on which temperate ecology has been constructed (Griggs, '34a) was it possible to make progress with the problem.

ARCTIC VEGETATION ESSENTIALLY MISCELLANEOUS

The vegetation of temperate regions is commonly described as made up of "associations" distinguished by characteristic plants regularly growing together. But in the typical plant communities of the arctic there are no distinctive plants. The most characteristic arctic species are ubiquitous and occur in many sorts of habitats, like the weeds of civilized countries. This has been discussed in its application to the arctic generally in the paper above cited and many specific examples will appear in the description of the more typically arctic types of the vegetation at Katmai.

The bewildering miscellany of plants characteristic of arctic habitats becomes more and more pronounced as the conditions become more extreme. In low arctic countries such as Katmai many habitats are transitional and partake of the character of the temperate zone. But in high arctic countries all habitats are occupied by the heterogeneous vegetation characteristic of the frigid zone.

The difference between arctic and temperate ecology may be epitomized in a word—competition and the lack of it. The closed associations of low latitudes maintain a certain definiteness of composition because the rigorous competition of the species present chokes all newcomers except those specially

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² I would here record my appreciation of the generous way in which the National Geographic Society has supported the scientific work of the Katmai Expeditions, both in the field and by way of grants to assist publication.

adapted to meet the conditions, *e.g.*, all seedling trees except beech, hemlock, and maple quickly perish from overshadowing in the climax forest of our northeastern states. In the arctic the plants, standing alone, spaced out in a very open vegetation, offer each other little or no competition and the plant cover has just such a character as would develop in temperate regions if every species whose seed fell in a given area became a part of the permanent vegetation.

The reason that the most abundant and characteristic arctic species occur in all sorts of habitats lies just here. Literally, they come up everywhere that their seeds fall. This of course does not mean that all the seeds produced germinate and persist. Far from it, for life in the arctic is everywhere precarious and few plants escape destruction for long. Rather it is to be recognized that destruction as well as seeding is indiscriminate, for the struggle for existence is dominated by the adverse forces of a frigid climate so that the plants perish before the competition characteristic of more favorable conditions has opportunity to develop.

It often appears, indeed, that the mutual shelter afforded by a bunch of close-packed plants more than counterbalances root and leaf competition. Thus many of the more delicate species are to be found only in the shelter of hardier neighbors, *e.g.*, on wind-swept Akpatok Island, a plant of *Dryas integrifolia* almost always forms the center of any spot of vegetation on the fieldmark (Polunin, '34).

ECOLOGICAL DISTINCTIONS IN THE ARCTIC NOT QUALITATIVE BUT ONLY QUANTITATIVE

Now by saying that arctic vegetation is essentially miscellaneous it is not intended to imply that there are no differences between the plant covers of different habitats. If that were so, the monotonous uniformity would present no problem to the ecologist. It is rather that the differences are elusive and variable. Vegetation differences in lower latitudes are qualitative in that different habitats are occupied by entirely different sets of species. But in the arctic the differences are merely quantitative. The habitat preferences (to use a figurative term) of the various species find expression merely in increased or decreased abundance in more favorable or less favorable habitats rather than by presence here and absence there. If one will take the time to chart representative quadrats in different areas, he will find that the differences may be expressed readily enough in relative percentages of the area covered by the characteristic species. If, however, he follow his quadrats through a series of years, he will find great changes from year to year and the changes from time to time, like those from place to place, are largely erratic.

The instability of arctic vegetation comes out with great clearness in unpublished studies by Palmer, Miller and Rouse of the reindeer pastures in Alaska. Studying intensively the grazed in comparison with the ungrazed

areas, first Palmer and later Miller and Rouse have established many permanent quadrats in different sorts of vegetation throughout the portion of western Alaska occupied by the reindeer industry. These have been followed, charted, and photographed over an interval of ten years, giving a basis for the interpretation of succession in the arctic not approached, so far as I am aware, by any other work. I must here acknowledge the courtesy of these workers and of the United States Biological Survey in permitting me to study and comment on their report. The instability of arctic vegetation, to be inferred from a single examination but demonstrated by these permanent quadrats, is due, of course, primarily to the heavy mortality in arctic climates and the subsequent repopulation of the area by chance seeding.

ARCTIC ECOLOGY BASED ON PHYSICAL HABITATS RATHER THAN ON ASSOCIATIONS OF PLANTS

As a consequence of the erratic character of arctic vegetation arctic ecology cannot be built on the assumption that the habitat affected by a plant gives a reliable indication of its optimum conditions. Inasmuch as this is the basic assumption which tacitly underlies a large part of current ecology in temperate regions, it is clear that arctic ecology must be built on a radically different basis. The feature which does vary from place to place, and is with some degree of consistency reflected by the vegetation, is the physical character of the habitat. Bog, feldmark, and heath are clearly differentiated physically and it is easy to see differences in their vegetation, though these differences are only quantitative. Arctic vegetation must therefore be described by reference to the physical conditions of the habitat rather than by an attempt to discover and deal with the habitat preferences of the species present.

IS THE KATMAI DISTRICT PROPERLY CLASSIFIED AS ARCTIC?

Further, although the Katmai district is beyond the limit of coniferous forest and lies therefore in the territory customarily mapped as arctic rather than Hudsonian or sub-arctic, yet the "climax" plant cover of the region differs from anything else described in the arctic and clearly belongs in the forest. The reason for this is that the forest in Alaska has not reached its climatic limit but is actively migrating into the arctic as demonstrated by the observations of many explorers and by detailed studies of the writer at Kodiak (Griggs, '34b). Comparison of the arctic timberline in Alaska with the alpine timberline in the Rocky Mountains shows that they are transitions of very different character. The timberline vegetation of Kodiak finds its proper comparison not with timberline in the Rocky Mountains but with the lower part of the Hudsonian zone many hundred feet below the limit of trees.

Throughout Alaska the last trees are erect and vigorous, not stunted and prostrate as on the mountains. Their growth is rapid in contrast to the very

slow growth of alpine trees. It is not infrequent for the last trees at Kodiak to increase more than an inch in diameter in a single year (Griggs, '34b, p. 83). Such rapidity of growth is unknown in the high mountains. On Sheep Mountain near Jackson, Wyoming, for example, I counted 287 rings in one of the last upright trees which had attained a diameter barely exceeding twelve inches. It was a large and successful tree. The dwarfed prostrate trees higher up the slope grew more slowly.

Again, the balsam poplar goes many miles beyond the spruces in the Katmai district, the last isolated outlying clump being found nearly 200 miles beyond the last spruce. But in the Rocky Mountains the balsam poplar³ does not ascend within several thousand feet as high as the spruce. Around Yellowstone Park, for example, this tree commonly drops out at about 6000 feet, while the spruces go up to about 10,500.

Finally, the herbaceous vegetation covering the ground between the last trees at Kodiak finds its counterpart in the Rocky Mountains not at timber-line but many hundred feet below it. In the country around Cooke City, Montana, for example, moderate altitudes around 9000 feet are occupied by an open forest where clumps of tall vigorous trees, subalpine fir and limber pine, come up in luxuriant mixed meadows of tall grasses and forbs in which *Geranium fremontii* is especially characteristic. The general character of the vegetation here is closely similar to the mixed meadows of the Alaska Peninsula in which the closely related *G. erianthum*, is a conspicuous member.

While all this is entirely anomalous on the supposition that vegetation is everywhere adjusted to climate, it is no more than the condition which should be expected from the demonstrated fact that the trees are migrating into the arctic.

In view of this situation a question may naturally be raised as to whether the Katmai district is properly assigned to the arctic. This also had to be settled before an account of the vegetation could be profitably undertaken. It is considered in detail in the earlier paper referred to ('34a) and there is no need of repeating the discussion. Suffice it to say that the arctic tree-limit is the only objective boundary which can be drawn around the arctic vegetation zone with any degree of satisfaction. Any attempt to delimit it otherwise results in a subjective or theoretical boundary which would be impossible to use in the field. Even though we recognize, therefore, that a thousand years hence much of our area will be covered with forest and so become Hudsonian, we must, pending such an event, definitely classify it as arctic.

LOCATION OF THE KATMAI DISTRICT

The Katmai district lies just beyond the border of the coniferous forest in southwestern Alaska. Beginning on the east at the head of Bristol Bay

³ I am aware that the balsam poplar of the Rocky Mountains might be given a different name from that of Katmai, but both are on the same continuous geographical range. See below, page 391.

and the village of Kodiak it covers the most of Kodiak Island and extends southwestward down the Alaska Peninsula toward the Aleutian Islands. Its outer, western, boundary is not a sharp line for, as in the arctic regions generally, transitions are negative rather than positive as the flora becomes poorer and poorer with increasing distance from the forest. In such cases definite lines are not to be drawn unless a single species is arbitrarily selected and its terminus taken for the boundary. The area is best defined as that in which *Calamagrostis scabra*, either alone or mixed with clumps of alder, occupies the best land in approximately pure stands. Thus defined it extends far down toward the Aleutian Islands. In a more general way the account here given will give a fair idea of the vegetation of much of the interior of Alaska, including even the more sparsely timbered areas or, more accurately, the open parks between the timber.

The writer's first opportunity to study the area came as a member of a party sent by the United States Bureau of Soils, in 1913, to survey the kelp beds of the region for a possible commercial source of potash. It was our daily practice after the day's work to anchor in some cove and go ashore at "night." Thus during the summer when daylight is almost continuous we were enabled to examine the vegetation at many places from southeastern Alaska to the Shumagin Islands in a detail not to be duplicated in many seasons' travel by ordinary passenger steamers. The work of this season entailed stops of several days each at Seldovia on the Kenai Peninsula near Cape Alitak, the southern point of Kodiak Island, at Mitrofan Bay, at Stepovak Bay, on the Peninsula, and at Sand Point on the Shumagin Islands. Later during the National Geographic expeditions there were many opportunities to study the normal vegetation outside the devastated area on the Peninsula both southwest of Katmai on the Pacific, around Naknek on the Bering Sea, and also on Kodiak Island.

In working up the vegetation I have had the advantage of access to the great collections of the Alaska flora in the National Herbarium and to the completed but unpublished flora of Alaska in the files of the same institution. The nomenclature and delimitation of species follows that work.

KATMAI VEGETATION UNTOUCHED BY HUMAN OCCUPANCY

One notable difference between the Katmai District and the corresponding areas of Europe from which most of our knowledge of arctic-alpine ecology is derived is in the almost total absence of human influence on the vegetation. In Europe wherever there is sufficient vegetation to support livestock, natural development of the plant associations has from time immemorial been greatly modified by the depredations of grazing animals.

In contrast to the countries of northern Europe, the whole of our area from Kodiak to Unalaska, a distance of 500 miles, is all but uninhabited. In former times the natives were very much more numerous than now, but they

were a maritime people gaining their livelihood largely from ocean and river. To be sure, they hunted and trapped ashore, but their only domestic animal was the dog and their effect on vegetation, except in the immediate vicinity of their houses, was negligible.

In this matter the student of Alaskan vegetation is most fortunate. It is not difficult to see how many things now clear would be greatly obscured if grazing animals abounded. Indeed, near Kodiak, where several ranches have been established of late years, haying and the selective grazing of animals have greatly modified the relative abundance of the species present, though there is as yet little change in the general aspect of the vegetation.

Again, in Alaska the vegetation is untouched by fire, thereby freeing us from a complicating factor which in many regions masks the normal vegetation, bringing about new climaxes which, except under the closest scrutiny, appear to be natural vegetation types.

CLIMATE

But the absence of population brings disadvantages as well as advantages to the ecologist. In an uninhabited country detailed climatic data are not to be had. Yet the rather meagre records of the nearest meteorological stations are, I think, sufficient to bring out the important characteristics of the Katmai climate.

The dominating factor in the climate of the Alaska Peninsula is a permanent area of low barometric pressure known as the Aleutian low. This gives the country a warm, windy, misty climate resembling that of Scotland, Iceland, and Scandinavia, which adjoin the similar North Atlantic low. The rainfall, which is evenly distributed throughout the year, amounts to about 60 inches, corresponding with that of Halifax, Iceland, Scotland, Norway, and Japan. The region lies just below the July isotherm of 10° C. (50° F.) which crosses southern Labrador, Iceland, North Cape, and Kamchatka. The winter temperature, i.e., the January isotherm, 5° C. (22° F.) corresponds with that of Nova Scotia, Iceland, North Cape, and central Japan. The extreme minimum of record both at Kodiak and at Unalaska is close to 0° F. The dates of the first and last frosts are very irregular from year to year but the interval between them averages about 150 days. On account of cloudy weather and low temperature, however, the country warms up slowly in the spring, so that willows and alders do not blossom until June.

Data are lacking regarding the important factors of snow and frozen ground. In the years when I have had opportunity to observe the southern side of the Peninsula the ground was still snow-covered in sheltered places in April, but snow melted everywhere on the lowlands early in May and by the middle of June was confined to gullies on the mountains from which it soon disappeared. By the first of July no snow is to be found except on glaciers or permanent névé which do not come below three or four thousand feet.

On the Bering Sea side the ground remains permanently frozen, as is the case further north. But on the Pacific side it always thaws out, sometimes well before the middle of June, sometimes not till after that date. At Kodiak all trace of frost is gone in May.

The Katmai district evidently has very much more rainfall than most arctic countries. The total precipitation in the Arctic Archipelago, northern Greenland, Arctic Russia, and northern Siberia is everywhere less than ten inches—over large areas of these regions very much less than ten inches. The temperature is likewise higher than in any part of these regions. The only arctic country closely comparable climatically with Katmai is northern Norway, which has very nearly the same temperature and nearly as much rainfall, distributed, moreover, in much the same way.

GEOLOGY

The Katmai district has been explored by a number of parties from the United States Geological Survey (see W. R. Smith, '25, and other bulletins there cited). There is no need here of entering into the detailed findings of the geologists. So far as the effect of the underlying rocks on vegetation is concerned, the most important fact is that most of the rocks of the region are silicious rather than calcareous in character and weather into soils which are acid in reaction.

In the northern corner of our area and extending far to the northward into the forested country beyond is a granitic batholith which is certainly older than most of the sedimentary rocks. The latter are prevailingly of Jurassic age with lesser areas of Cretaceous and Eocene as well as a small area of Triassic. In the Jurassic there are great masses of conglomerate, in places 900 feet thick, composed of large granite boulders together with arkoses, coarse sandstone, and some shale to the thickness of more than 10,000 feet. Through these strata, still lying for the most part nearly as level as when they were laid down, have broken eruptive rocks of the volcanic chain, the backbone of the Peninsula. These are mostly intermediate in silica content.

The geology of Kodiak Island is little known. There are great masses of highly metamorphosed slate and graywacke with intrusive masses of granite, all supposed to be Mesozoic.

FLOWER BIOLOGY

The outstanding characteristic of arctic-alpine forbs, as is well known, is the large size and bright color of their flowers. Often the flowers are almost as large as all the rest of the plant above ground. Harebells with corollas 20 mm. long rise on short stalks from rosettes of leaves only 15 mm. long. Little plants of *Primula cuneifolia* in diminutive rosettes whose leaves are only 10 mm. long may bear two or three bright pink-purple flowers measuring 12 mm. Were such flowers to appear from underground bulbs there would

be no occasion for surprise, but bulbous plants are few and in these species as well as many more of similar character, food storage organs are only slightly developed. Research into the causes of the large size of arctic flowers might be undertaken with profit. If the secret were discovered it might prove of value to florists and others interested in producing ornamental plants. Certainly it is not, as is commonly supposed, a simple matter of altitude or latitude. An illustration will make this clear. Kodiak and the Pribilof Islands are at sea level at about the same latitude. To a large extent the same species of plants grow in both places. But on the Pribilofs the flowers are notably larger than on Kodiak. Careful analysis of the climatic differences ought to suggest experimental procedures by which similar differences might be produced under greenhouse conditions.

All sorts of flower types are represented at Katmai: there are numerous radiate flowers like anemones, buttercups, and chrysanthemums and many specialized irregular types such as *Aconitum*, *Pedicularis*, *Mimulus*, *Cypripedium* and other orchids. Nor is any particular color much more evident than others. There are yellow *Potentillas* and *Sieversias*, *Calthas*, *Arnicas* and *Saxifrages* (*S. flagellaris* and *S. hirculis*); red-purple *Rhododendron*, *Pedicularis*, *Silene acaulis*, *Saxifraga oppositifolia*, and the fireweeds, *Epilobium angustifolium* and *E. latifolium*. For blues there are *Polemonium acutiflorum* and *P. humile*, *Myosotis alpestris*, *Lagotis glauca*, *Aconitum delphinifolium*, *A. maximum*, *Aster sibericus*, *Campanula alaskana*, and *C. lasiocarpa*, so that blue must be accounted as being as well represented here both in variety of species and in abundance of individuals as any other color, instead of being deficient or entirely absent as is sometimes reported in the arctic.

Bumble bees and syrphid flies are abundant both on the tundra and on the feldmark. They were the only insects observed visiting the flowers. However, they probably serve as effectively as pollinators as would a greater variety of insects.

BERRIES

As to the quantity of berries produced on the tundra there is considerable variation from year to year. In five of the six summers I have spent in the country there were few berries but in the sixth they were plentiful, but not profuse. The chief producers were *Vaccinium uliginosum*, *Empetrum nigrum*, and *Rubus stellatus*. Although *Vaccinium vitis-idaea* is one of the commonest plants on the tundra I have never seen a place where I could gather a handful of berries from it. *Rubus chamaemorus*, *Viburnum pauciflorum*, and *Oxycoccus palustris* are hardly abundant enough to permit a fair estimate, but my impression is that *Rubus chamaemorus*, the "baked-apple berry," fruits freely, while the "cranberries," both high bush and low bush, do not. This is in contrast to the abundant berries of Labrador, arctic Russia, and Siberia as reported by observers in these countries. Further east, within the borders of the forest at Kodiak, where other species of berry-bearing

plants, *Rubus spectabilis* and *Vaccinium ovalifolium*, occur, berries have been exceedingly abundant in every year of my experience.

ECOLOGY

As in other regions there are several pioneer habitats from which transitions lead, by different stages, toward the climax association. Succession may start from the beach (psammosere), from ponds and streams (hydrosere), from rocks which give rise to acid soil (oxysere), or to soil that is alkaline to neutral (alkisere). The relations of these varied series may best be understood from a schematic representation of the transitions such as is given in the diagram (fig. 1).

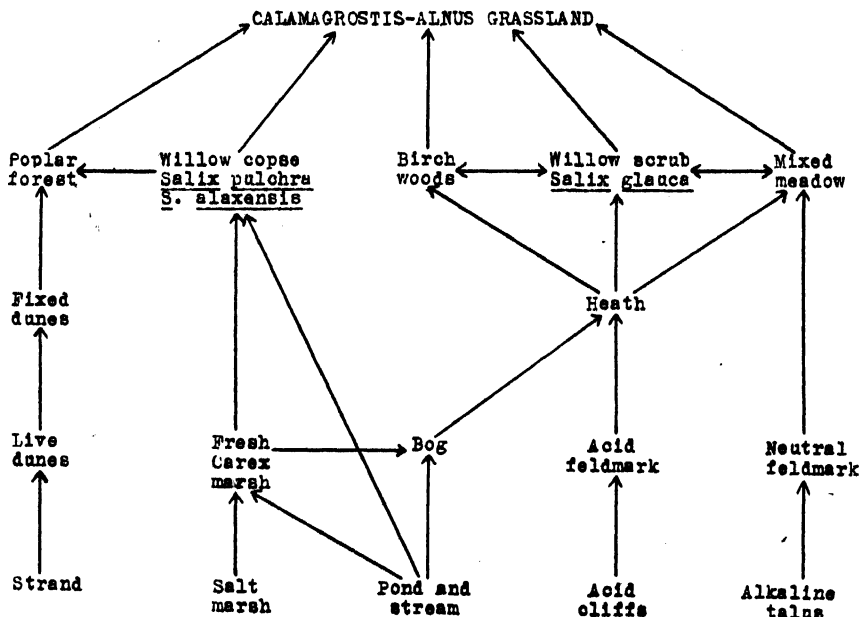


FIG. 1. Diagrammatic representation of the plant succession in the Katmai region.

It is to be observed from this table that while the lower members of the series, including the types more typically arctic, are best described in terms of habitat without reference to plant cover, the higher, which are transitional to temperate types, are characterized by naming prominent plants. Of these the climax (or better the subclimax), the alder-grassland, is a true association in the temperate sense that there competition excludes intruders and thus maintains the purity of the plant cover as in a beech forest in lower latitudes. In the intermediate meadows, the poplar forest, the birch forest and the mixed forb meadow, the presence or absence of any of the "character" plants named has little effect on the rest of the vegetation. That is to say, they are not character plants in the proper sense of the word but yet are convenient to use for descriptive purposes.

THE STRAND, PH 7

The vast quantities of volcanic sand washed down to the sea by Katmai River during the eighteen years between the eruption and the time these observations were made has greatly increased the beach area and augmented the importance of sand-binding plants. New bars were built up half a mile to seaward from the old beach and so gave an exceptional opportunity to follow the colonization and stabilization of new sand. The first pioneers were *Honkenya peploides* var. *oblongifolia*, *Lathyrus maritimus*, and *Mertensia* [= *Pneumaria*] *maritima*.

On the most rapidly growing of the new beaches *Mertensia* was less common than the other two but was present and thrifty. On older beaches it sometimes reached considerable size. One mat 130 cm. across was measured. There were two forms, one with blue flowers, dark foliage, and dark brown fruit, the other with white flowers, pale foliage, and yellow-green fruit.

While *Honkenya* and *Mertensia* were rather closely confined to the beach, *Lathyrus*, in Alaska as elsewhere, is abundant also back of the strand, scrambling in rank growth over the dune grasses.

In quiet coves and in more sheltered places on the outer beach also are patches of *Senecio pseudo-arnica*.

In spite of the high winds characteristic of arctic countries sand dunes are seldom as well developed as in lower latitudes, perhaps because the ground is frozen so much of the time. In this respect southwestern Alaska is exceptional, partly because of the enormous quantities of loose volcanic ash.

Along with the first successful pioneers on the strand come individuals of *Elymus mollis* [= *E. arenarius*]. But these attain no considerable size until blowing sand has built hummocks well above the reach of ordinary storms. As larger dunes are formed they are promptly occupied by this grass in pure stands.

The efficient runners of the grass enable it to surmount sand drifts that smother all other species. Its roots reach great depths. I have found them at the base of a cut bank seven meters high, and even so deep a cut did not uncover their tips which had reached still further down. Near the surface they interlace closely and effectively hold the sand against wind movement. But they cannot withstand wash by tidal currents (fig. 2).

Like several other dune grasses such as *Ammophila arenaria* and *Uniola latifolia*, *Elymus mollis* is further adapted for its extreme position on the dunes by deep fluted grooves on the upper side of its leaves which permit them to roll up and reduce transpiration when the wind is too severe.

Among sand-binders *Elymus mollis* must take high rank. Katmai beach, standing athwart a funnel-shaped valley leading back across the mountains, has a well deserved reputation for the violence of its gales. Ever since the eruption the ash, both that which fell directly on the dunes, amounting to from 30 to 100 cm. on the level, and that from the more heavily covered country up-valley has continued to blow and accumulate in enormous quantities.

Inland where *Elymus* does not occur unstable dunes of shifting ash are frequent and are the chief deterrent to revegetation, but within the range of beach grass blowouts are few, and loose, unanchored sand is confined largely to the beach alone.

Although *Elymus mollis* does not go far from the seashore it is not confined to the strand. Thrifty patches of it occur in residual shale on the mountain sides above the beach to an altitude of 1000 feet. It goes inland only about a mile, as far as the ruins of Katmai village, but it occurs in tidal marshes as well as on the dunes.



FIG. 2. A small sand dune washed out by high tides revealing the matted underground parts of the beach grass, *Elymus mollis*.

In places along the front of the dunes where the sand-drift is less active, plants from the strand, especially *Lathyrus maritimus*, creep in among the culms of beach grass.

On the back of the dunes and on older dunes where the sand has been thoroughly stabilized and humus has begun to accumulate, the reaction shifts toward the acid side, reaching about pH 6. As this occurs *Elymus* is gradually replaced by a mixture of grasses and forbs similar to that on the margins of the dominant grassland, or *Elymus* may give way directly to *Calamagrostis* or to poplar forest. The plants of old dunes include: *Epilobium* [= *Chamaenerion*] *angustifolium*; *Polytrichum*, *Hylocomium* and other mosses; *Trien-*

talis europaea arctica, *Solidago lipida*, *Achillea borealis*, *Galium boreale*, *Fritillaria camschatcensis*, *Populus trichocarpa*, *Calamagrostis scabra*.

THE RIVER-BANK POPLAR FOREST, PH 6

Poplars in Alaska occupy very much the same place in plant sociology that they do in lower latitudes. They come in at an early stage in the succession, especially on gravel banks along the streams, and in places form large and luxuriant forests. Yet here they are not confined to new habitats as they are further south but occur also in mixed grassland beyond the pioneer stage of succession or even to a limited extent on the heath.



FIG. 3. Typical hummocks and hollows of the heath.

A most extensive and well developed poplar forest formerly occupied most of Katmai Valley, which was a broad flat of glacial outwash gravel. This forest, covering perhaps 50 square miles, was destroyed by the eruption, but enough remains in nearby valleys and elsewhere to complete the picture of former conditions.

The trees here are "Balm of Gilead," continuous geographically with both balsam poplar of the interior, *Populus tacamahacca*, and with the coastal cotton-wood, *P. trichocarpa*. The two are indistinguishable in this region except by their capsules which are glabrous or hairy, respectively. Authenticated specimens of both from Kodiak are preserved in the National Herbarium. Yet I doubt if it could be seriously maintained that the poplars of Kodiak belong to two species. Our tree is one of those transitional forms which does not fit satisfactorily into current conceptions of species.

While the poplar forest is one of the most conspicuous types of plant cover in the region it has little significance as an ecological unit. The poplars are simply superposed on the ground vegetation. That is, on rich alluvial lands they merely grow through the *Calamagrostis*, which occupies the ground almost as though the trees were absent. On mixed grassland or even on grassy heath the poplars, there much gnarled and stunted, protrude through a vegetation which, if the trees were cut down, would be difficult to distinguish from adjacent treeless tracts (fig. 8).

Similar conditions are general in other arctic woods beyond the line of conifers. Thus in Finnmark, Leach, and Polunin ('32, page 417) after dividing the vegetation into two associations, the birch forest and the heath, add: "Whether this division into two associations is a legitimate one or not is a debatable point, as for the most part the only constant difference between them is the presence or absence of birch trees."

In the Katmai district the poplars reach a comparatively large size, commonly exceeding fifty feet in height and occasionally living until their trunk may exceed a meter in diameter. The largest seen measured 4.15 meters in circumference (fig. 4). The increase in height in well-grown leading branches here varies from 10–18 inches (25–45 cm.) per annum, averaging about 14 inches (35 cm.). Ring counts show that trees require about a century to reach a diameter of a foot (30 cm.), though individual saplings sometimes grow much more rapidly. One six inch tree was only 17 years old, *i.e.*, with growth rings of .18 inches (4.4 mm.) against a general average of about .06 inches (1.5 mm.).

The poplar is here near the geographical limit of its range so that the poplar forest is necessarily of limited importance. Within a very few miles west of Katmai it ceases to be a factor in the vegetation. Isolated patches, however, occur for nearly two hundred miles to the westward. The last known clump, consisting of about sixty trees, is reported by Knappen ('29), on the Bering Sea side of the Peninsula north of Chignik, approximately in longitude 158° 30', latitude 56° 40'. Further east it is displaced by the spruce, which soon crowds the poplar out of all but the newest land, such as river bars and outwash flats below the glaciers.

THE SALT MARSH

Low coastal flats occasionally overflowed by the tide here as elsewhere develop a specialized plant cover distinct from that of other habitats. The salt marshes of southwestern Alaska may be very briefly described as practically pure stands of one grass, *Puccinellia paupercula alaskana*.

Other species present are so scarce that they may be neglected in an ecological discussion. The only plants at all common are *Triglochin palustris* and an atriplex, probably *A. alaskensis*. The familiar halophytes of salt marshes further south do not extend into our region. The nearest record for *Salicornia*, for example, is Cook Inlet.



FIG. 4. A giant poplar in Katmai Valley killed by the eruption.

ACID FELDMARK, PH 6

A second succession, the oxysere, starts on small rocky hillocks standing above the general level of the dwarf shrub heath where the bedrock stands a few feet higher than usual and where the snow is blown off and the vegetation is exposed to the wind most of the winter. Such knolls are occupied by pioneer heath plants consisting especially of *Andromeda polifolia*, *Loiseleuria procumbens*, *Vaccinium uliginosum*, *Salix arctica*, *Lagotis glauca*, *Ledum decumbens*, *Campanula lasiocarpa*, *Arctostaphylos alpina*, *Artemisia arctica*, *Arnica lessingii*, *Aira caespitosa*, *Senecio resedifolius*, *Vaccinium vitis-idaea*.

Areas of this type show a large percentage of bare rock and the plants are killed back at frequent intervals. The stems of the largest plants in a typical habitat of this sort when examined in cross-section had only nine rings of growth. That is, they had been killed back at least once since the eruption. The severity of conditions is reflected by the condition of *Andromeda* here as compared with the plants of New England bogs, *A. glaucophylla*, which were long considered the same species. Here it is a diminutive dwarf rising only 2-3 cm. off the ground in contrast to the relatively gigantic plant of the bogs, which is ten or twelve times as large. Exposure to high winds and periodic desiccation favors bodily removal or complete oxidation of the scanty plant remains and little or no humus is formed. If conditions were a little less severe, humus would accumulate and the more vigorous plants of the adjacent heath would overgrow the habitat.

Vegetation like the acid feldmark is a typical development in similar habitats throughout the arctic. In low arctic countries like ours it is of limited extent but in the high arctic it becomes the characteristic feature of the country. Some authors, e.g., Lippmaa ('29), Esthonia, call them heaths; others like Hansen ('30), Iceland, term them fellfield, fjaeldmark or feldmark. The latter term would seem more appropriate even though the characteristic plants belong to the heath series, for the habitat most resembles feldmark as reported elsewhere. Nowhere else in the arctic, so far as I have found, have ecologists divided vegetation of this type into alkaline and acid feldmark, as is necessary at Katmai (see below), but the strong soil preferences of alpine plants were noted and commented upon long before hydrogen-ion concentration was recognized as an ecological factor (Fernald, '07).

Despite the close similarity in appearance between the acid and the alkaline feldmark at Katmai and the fact that they shade into each other as the reaction shifts, they are very definitely distinct ecologically as well as floristically, for their place in the succession is different. The one leads to heath and the other to grassland.

THE HEATH, pH 5-6

Poorly drained plains, especially those covered with Pleistocene glacial outwash, are usually occupied by a varied dwarf-shrub heath which is more like the "moss tundra" of the more northern parts of Alaska than anything else in our region. Extensive areas of this heath have been studied by the writer at several places: between Katmai and Kashvik Bays, on the Pacific side of the Peninsula; around Nakenk River and Lake on the Bering Sea side; near Cape Alitak on Kodiak Island; on the Shumagin Islands; and in southeastern Alaska between Yakutat Bay and the Alsek River. The Yakutat area is intermediate between our heaths and the bogs of lower latitudes.

In the heath of this region *Empetrum nigrum* usually occupies half the ground or even more. With it are *Vaccinium uliginosum*, *Betula rotundifolia*, *Ledum decumbens*, *Vaccinium vitis-idaea*, *Salix arctica*, *Arctostaphylos*

uva-ursi, *Calamagrostis scabra*, *Pedicularis capitata*, *P. artica*, *Cornus suecica*, *Epilobium latifolium*, *Petasites frigida*, *Carex* spp. (nearly always sterile), *Chrysanthemum arcticum*, *Artemisia arctica*, *Rubus stellatus*, *Parnassia palustris*, and *Swertia perennis*, together with an abundance of large fleshy fungi, especially of the genus *Boletus*. These are at times, here as elsewhere in the arctic, the largest and most conspicuous plants of the habitat.

The composition of the heath is very indefinite. The relative abundance of the component species is never twice the same. The most conspicuous variant is *Betula rotundifolia* which may even vie with *Empetrum* for first place. Further complicating the situation is the fact that the heath shades indefinitely into all the neighboring vegetation types: not merely meadow and feldmark but bog, bushland, and forest as well. Transitions, in fact, occupy more ground than areas which could be called typical.

It should be pointed out in discussing this, the most characteristically arctic portion of our area, that the lower plants, mosses and lichens, commonly associated with tundra in the popular mind are of very subordinate importance on the tundras of southwestern Alaska. Only in one area, and that far from Katmai, have I seen any abundance of cladonias—the reindeer moss of the area further north. The exception was in the exceedingly rainy, cloudy country of Prince William Sound far within the forest. There cladonias are sufficiently common to become a noticeable feature. Mosses of many kinds are of course common but they are never dominant and assume little more importance in the vegetation than in the forests of lower latitudes. Nowhere in this region are they abundant enough to justify a description of the tundra as a “moss-covered plain.”

Three other significant absences from the heath should be mentioned: *Cassiope tetragona*, which in the high arctic replaces *Empetrum* as the most abundant heath plant, does not occur here. *Salix glauca* likewise, though abundant in adjacent scrub, does not enter the heath here as in Greenland but is strictly excluded from it. *Dryas* is commonly a characteristic plant of either heath or feldmark but I have not observed it in the Katmai district although there are specimens of *Dryas octopetala* from our region in the National Herbarium and it is common in Cook Inlet.

HUMMOCKS AND HOLLOWS OF THE HEATH

Quite as characteristic of the heath as its plant cover is its peculiar hummocky surface. Everywhere it is thrown into a remarkable system of steep-sided ridges and intervening hollows. The pattern they make is very irregular but where best developed the ridges form a continuous network surrounding the circular holes (fig. 3). These vary greatly in size. They are commonly two or three meters or more, though often no more than a meter, in diameter. In depth they frequently exceed a meter and in extreme cases a man slipping into one may almost drop out of sight. The bottoms are soft

mud, often paved with loose angular stones. In wet weather they may stand covered with water for long periods (fig. 5). Consequently vegetation is sparse or absent on the bottom. The ridges, on the other hand, carry the most vigorous plants of the heath and because of this difference the ridges are continually being built higher and higher by the accumulating plant remains. There is reason to suspect also that the hollows are slowly bored deeper year by year by the action of the ice which accumulates in them during the winter. One can therefore distinguish older from younger heaths by the rougher surface.

Curious surface markings probably more or less related to those at Katmai are characteristic of arctic lands generally. They differ considerably, however, in different regions. In interior Alaska the tundra is dotted

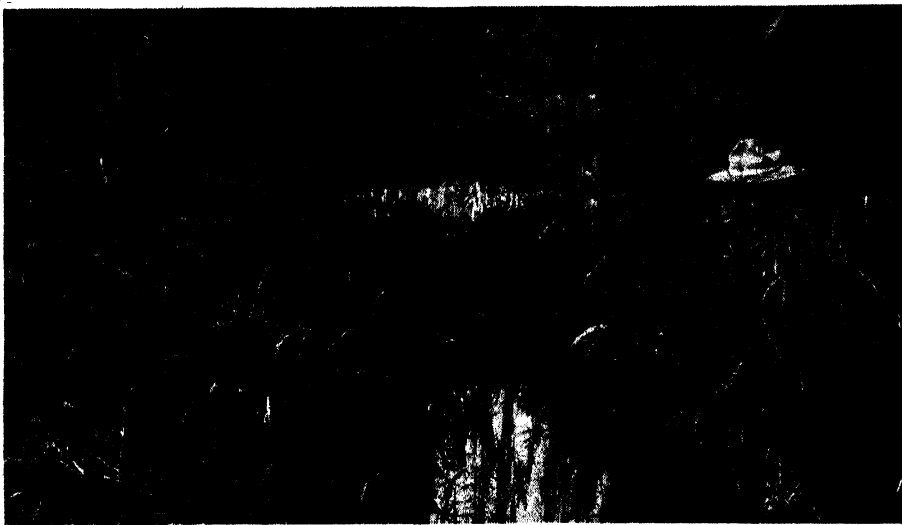


FIG. 5. Hollows in the heath filled with water; in August.

with tussocks known as "niggerheads" from the black matted appearance they present when the intervening hollows are covered with snow. The "knolls" of the "mo" vegetation in Iceland as described by Hansen ('30), seem to be similar to the niggerheads of America. In Iceland these knolls are more characteristic of the widespread "mo" vegetation than are the plants which grow thereon.

More closely related, perhaps, to the meshwork of ridges at Katmai are the "mud polygons" and "stone polygons" of many arctic and alpine regions but especially studied in Spitzbergen (see Elton, '27, and the literature there cited). Despite a great deal of thought spent by a number of writers in the effort to interpret them, knowledge of these features has not passed over from the stage of speculative a priori reasoning to that of experimental demonstration. Nearly everyone who has commented on them has taken oc-

casion to stress the need of more thorough study and certainly my experience leads me to join in this sentiment.

The deep hollows between the ridges found at Katmai differ from any other arctic soil features that I have seen reported. But in the mud polygons, and to a lesser extent in the stone polygons, plants are often restricted to the marginal areas, so that as at Katmai the vegetation emphasizes the reticulate structure of the ground. This feature is especially well shown by one of Polunin's pictures of Akpatok Island, 1934.

Retardation of vegetation in the hollows at Katmai seems to be due to two factors, lack of drainage and snow and ice effects. The importance of lack of drainage will be discussed more fully presently and here it need only be pointed out that standing water which fills the hollows for many days considerably shortens the period of growth. Snow which must lodge in the hollows during the winter has the same effect, for ridges are free of snow long before it melts out of the hollows, so presumably they have a growing season several weeks longer.

It may not be wise to speculate as to the effect of freezing on the ridges, but it is clear that in so far as the snow in the hollows becomes ice its expansion must exert a compressive action which would tend to squeeze the intervening ridges higher and higher. This push would be very effective if perchance the soil of the ridges at the time were unfrozen and so freer to yield to pressure. The occurrence of such a condition seems altogether likely because of the insulating effect of the plant cover on the ridge which would keep the soil beneath from freezing until long after any water in the hole had solidified. The reverse effect may be seen in summer when a block of frozen ground may sometimes be found in a ridge long after frost has disappeared everywhere else (fig. 6). A similar effect is figured by Elton in Spitzbergen where summer thawing goes much deeper in the bare centers of the mud polygons than in the plant-covered margins.

Among the species of the heath there are marked differences in ability to overcome the unfavorable conditions in the hollows and to extend into them. Some of the more open depressions are covered with a thick carpet of foliose liverworts, especially *Cephalosiella byssacea* (Griggs, '33). These are dark brown or almost black after a period of dry weather but quickly turn green after a week or two of rain. Some of the very narrow holes are literally filled by a bushy, much branched willow, rooted, not in the bottom, but high up on the side of the depression. This is doubtless a snow reaction similar to that of the alder in better drained situations.

Of the heath plants proper, *Vaccinium uliginosum* and *Arctostaphylos uva-ursi* show a marked tendency to occupy bare hollows into which the other plants cannot follow. Both of these are known in other arctic regions as characteristic of habitats covered late by snow banks.

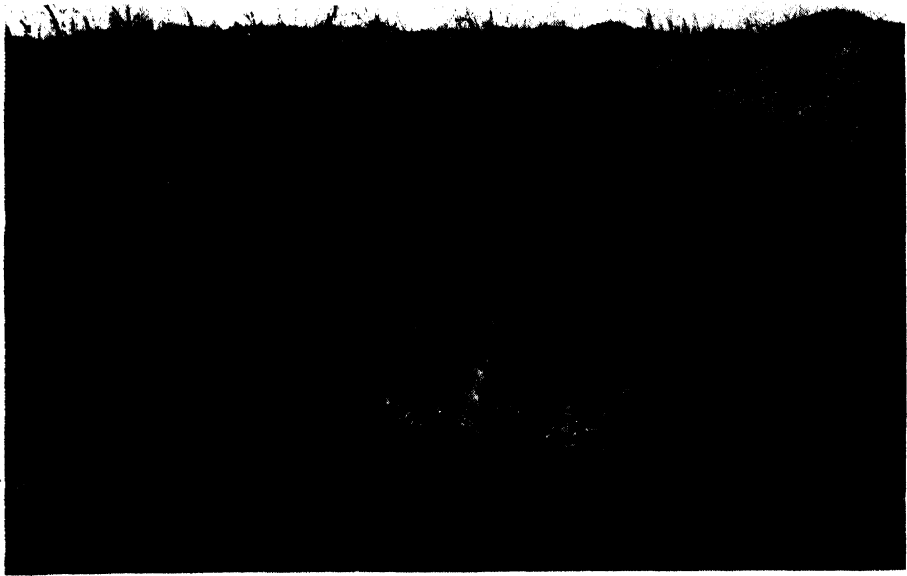


FIG. 6. A section of a tundra ridge late in June, 1917. The lighter central area is frozen soil. The surface has thawed to the depth of about a foot while the soil under the frozen mass was possibly never frozen at all.

LACK OF DRAINAGE A CRITICAL FACTOR IN THE HEATH

By far the most important factor in the development of the heath appears to be lack of drainage. Heath occurs only on flat, poorly drained plains. Wherever, locally, better drained situations occur, a grassland usually with trees or bushes comes in. Hillocks projecting above the general level, provided they carry sufficient soil, are crowned with islands of the *Calamagrostis* grassland (fig. 7). Along a trail the effect of drainage is occasionally brought out even more clearly. Where travel has worn deep into the matted heath vegetation the rut thus formed becomes a drainage ditch which carries off the water from the immediate vicinity. In such places the trail is marked by a fringe of grass (fig. 8).

Drainage does not, however, necessarily involve dryness. The good effects of drainage may be observed in situations even wetter than those suffering from lack of drainage. A pond in the tundra near Katmai was surrounded by a narrow fringe of grassland. The grass was very much wetter than the heath which invested it, yet it must be described as better drained. Stream banks in the tundra often bear a similar narrow fringe of grass which promptly gives way beyond the influence of running water. Similar conditions are described in northern Scandinavia (Fries, '13). It is not water but *stagnant* water that is deleterious. The difference probably lies in the oxygen content. The stagnant water of heath and bog, percolating through masses of decaying vegetation, is probably very poor in oxygen, while water stirred up by waves or currents would have opportunity to ab-



FIG. 7. An island of *Calamagrostis* on a well drained hillock of the heath surrounded by a mixed meadow with *Salix glauca*.

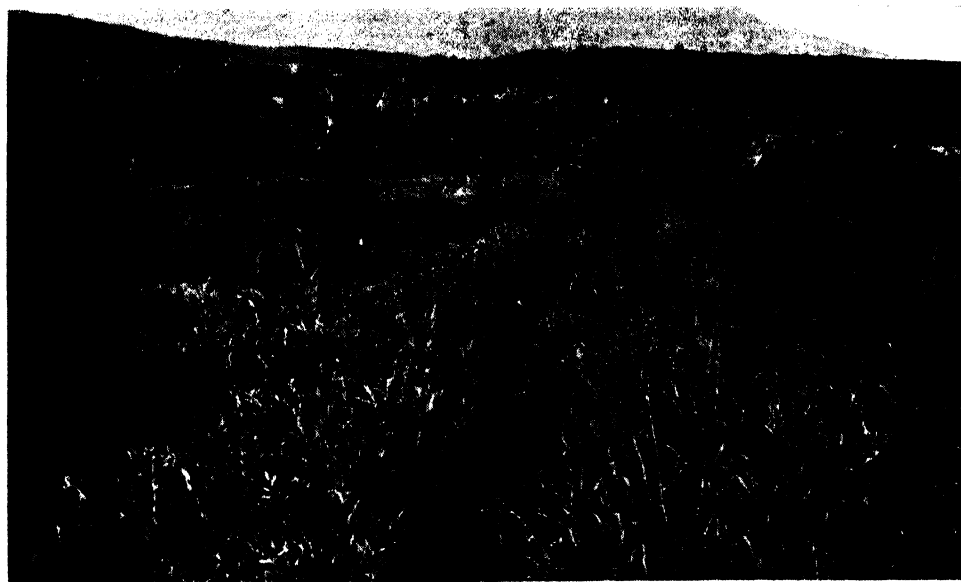


FIG. 8. A trail in the heath acting as a drainage ditch with its border of *Calamagrostis*. There is *Sphagnum* in the trench and *Empetrum* on both sides. In the background the heath gives way to a stunted poplar forest where the greater slope permits better drainage.

sorb it. Aeration has been shown by many writers to be of the utmost importance in the development of roots. Heath and bog conditions are generally supposed to be due to acidity but in the Katmai district where most terrains are acid to about the same degree aeration appears to be far more important than acidity.

RELATION OF KATMAI HEATHS TO VEGETATION OF OTHER REGIONS

It is the type of vegetation which I am calling heath in contradistinction from grassland or forest to which the Alaskans refer when they speak of "tundra." It is more closely related to bog than to any other vegetation type in the temperate zone of America. But Europeans would more readily recognize its relationship to heath, and it is from them that I have borrowed the designation used, yet our terrain is neither typical heath nor typical bog but intermediate between them.

In any case it does not seem best to follow those who would restrict tundra to such boggy places, for the best usage of that term (Griggs, '34a) seems clearly in a broad geographical sense to cover all arctic vegetation of whatever type.

Travelling north into Alaska one finds himself calling all habitats resembling the heaths of Katmai "bogs," because of the very gradual transition from the bogs of the States to the tundras of southwestern Alaska. Yet our heath is not a bog. There is little or no sphagnum⁴ except in places transitional to bogs and little or no peat such as develops in a bog. Furthermore, real bog as well as heath occurs in the tundra. (See below.)

From the typical heaths of northern Europe, however, ours differs both floristically and ecologically. It is very much wetter and there is neither *Calluna* nor *Erica*. Its shrubs are all strictly dwarfed forms which rise only a few inches off the ground in contrast to the high bushes of the European heath. Superficially, the heaths of Scotland, the grouse moors, may appear to be covered with dwarf shrubs but it should be remembered that there the dwarf shrub effect is artificially maintained by systematic burning every few years. But our heath is a primeval formation untouched by man, either with fire or in any other way.

HEATH A PERMANENT SUBCLIMAX DUE TO LACK OF DRAINAGE

The great height attained by the ridges in the heath makes it clear that they have been long in the building and that the heath is old. Transitions to the heath from other vegetation are abundant but they represent static variations in the conditions of the habitat which affect drainage, etc., rather than dynamic moving vegetation fronts. While the grasslands probably have behind them a successional history of greater or less length, the heath probably came into

⁴ Sphagnum becomes less and less important northward. Thus in Spitzbergen Sumnerhayes and Elton ('23), found sphagnum only in one local habitat.

its present position very shortly after the ice age with no more than a transitory feldmark intervening. Clearly, if drainage were improved the heath would soon be supplanted by other vegetation, but what is to improve drainage on a flat plain? A more likely event would be a warming up of climate, which would reduce the amount of stagnant water and so permit mesophytic plants to come in.

The heath has developed under conditions unhealthy to ordinary plants, perhaps unhealthy also to the heath plants though tolerable to them. So it is to be regarded as due to something like a diseased soil. In its southern extensions on the Pacific side of the Peninsula heath develops only in localities most unfavorably situated for drainage and so is of limited occurrence. But further north on the Bering Sea side and in the interior where the climate is more unfavorable, causing a permanently frozen soil and a slower snow melt, both of which interfere with drainage, heath is much more widespread and occupies much country. At Katmai the "disease" is acute but further north it becomes chronic.

AQUATIC SUCCESSION

In the arctic, as in temperate regions, new ground is being formed continually by the filling of ponds and so there is a similar succession from hydrophytic to mesophytic communities, especially from pond to heath. Yet it is probable as a matter of history that most of the heath developed the other way from bare rock detritus, either through the acid feldmark or, in the less exposed habitats, directly from bare ground. But however that may be, all intermediates between the vegetation of open water and the heath are frequently seen and may be conveniently described in ascending order.

Plants of Open Water

The innumerable ponds which dot the tundra, like the waters of most arctic districts, are poor in plant life as compared with similar habitats further south. Those in the area most affected by Katmai volcano remain, moreover, poorer than before the ashfall. The eruption, occurring on June 6 before the aquatics had resumed their vegetative summer condition, caught the hibernacula of the water plants on the bottom and buried them under a layer of ash from which they could not emerge. There is thus rather a long list of plants collected before the eruption which have not been seen since that time. These are *Potamogeton pusillus*, *P. filiformis*, *P. interior*, *P. perfoliatus*, *P. alpinus*, *P. heterophyllus*, *Ruppia maritima*, *Callitriche autumnalis*, and *Utricularia vulgaris*. The number of these plants suggests that there was formerly an aquatic vegetation much richer than expected in a country whose terrestrial plant cover must be classified as arctic.

The present aquatic vegetation occurring in several types of habitat may be dealt with very briefly:

A. Pools along the rivers or muddy banks are occupied by *Ranunculus hyperboreus*. *Batrachium* sp. has also been seen in this situation. Probably the preeruptive vegetation of such habitats was richer.

B. Brooks in the poplar forest with circumneutral water, pH 7.5, may have several aquatic mosses (Hypnaceae) with *Potentilla* [= *Comarum*] *palustris*, *Menyanthes trifoliata*, and showy mats of *Caltha palustris*. *Comarum* and *Menyanthes* also occur in bog pools, but *Caltha* does not follow them into such habitats.

C. Ponds may be occupied by a thick growth of water lilies, *Nymphaea polysepala*, which on account of their strong growth and the large amount of reserve food in the rhizome survived burial under rather heavy deposits of ash. The water lilies are here at the limit of their range and while they occupy nearly every pond at Kodiak within the borders of the forest they appear on the tundra only occasionally. Where water lilies fail the only aquatic seed plant in the ponds may be *Sparganium minimum*. Where the pond is small and stagnant without wave action it may be bordered by a fringe of *Hippurus vulgaris* and *Menyanthes trifoliata*, which pass directly into the bog. But in larger ponds where waves keep the bottom stirred up the bog does not come down to the water and an intermediate belt of sedges develops.

The Sedge Marsh, pH 8

The pond margins are usually invaded by a zone of sedges, especially *Carex lyngbyei*,⁵ which grows tall and rank, stretching its rhizomes out until deep water stops further progress. Beyond the sedges may be a greater or less development of *Sparganium minimum*.

Locally the sedge border has become of great importance since the eruption. *Carex lyngbyei* in pure stand or with a lesser amount of *C. stylosa* has colonized several square miles of alluvial ash flats built up in the lagoons at the mouth of Katmai River. Upriver wherever a bar for a time escapes washing away by the shifting braided channels of the overloaded river it is colonized by these sedges.

Before colonization these ash flats had a dry, hard-packed surface quite different from the muddy pond margin and were not favorable for plants. Seven years after the eruption the flats were still quite bare. But once started the closely standing culms spread rapidly and prevent drainage on the flat, which is nearly level, and transform the hard, dry surface into a soggy marsh ankle-deep with standing water. It is a notable case of the reaction of a habitat to its plant cover.

As stated, the sedges are in pure stands. They allow no competition except along the unoccupied edges where new pumice has been recently piled by the streams. Here occur several species from the strand and salt marsh: *Elymus mollis*, *Puccinellia paupercula alaskana*, and *Triglochin palustris*.

⁵ The specimens of *Carex* were kindly determined for me by Mr. E. C. Leonard of the National Herbarium.

These are all to be classed, I believe, as ephemeral waifs rather than as true pioneers.

Landward where the slope becomes a little greater and the banks are better drained the sedges give way to one of the other associations depending on the conditions of the habitat. A willow copse, a bog or even the climax grassland may come in, depending largely on the lay of the land.

The Willow Copse

On river flats the sedge-land usually passes over into a series of thickets arranged in zones according to drainage. Farthest into the marsh go the bush willows, *Salix pulchra* and *S. richardsonii*. These on dry ground are replaced by the tree willow, *Salix alaxensis*. Even further out in the marsh than the willows *Calamagrostis scabra* comes in and becomes increasingly luxuriant as the sedges are left behind in passing to better drained ground. Here the willows give way to poplars and we have the poplar forest already described.

The Bog

Where the land at the inner edge of the sedge zone is more poorly drained than among the sedges themselves—not where there is more water but where there is less movement of water—the sedges give way to a bog. When one looks *across* one of these bogs it has the aspect of a meadow from the number of sedges and grasses that grow through it. But when one looks *down* at the surface on which he stands it appears little different from an ordinary sphagnum bog as seen further south; that is to say, the tall grass-like plants stand far apart and make a rather small percentage of the whole plant cover.

The basis of the bog is sphagnum, in which grow a large variety of plants, including *Carex hindsii*, *C. limosa*, *Eriophorum callitrix*, *Myrica gale*, *Salix reticulata*, *Vaccinium uliginosum*, *Betula glandulosa*, *Salix ovalifolia*, *Calamagrostis scabra* (small), *Rubus chamaemorus*, *Saxifraga hirculis*, *Betula kenaika* (one foot tall and less), *Empetrum nigrum* (scarce), *Potentilla palustris*, *Oxycoccus palustris* (scarce); *Polytrichum* and other mosses.

Of these plants the *Myrica* is very characteristic and the *Rubus chamaemorus* and *Saxifrage* are not found outside the bogs. Thus though they never make any large fraction of the vegetation, they are among the very few species of this region which are confined to single habitat.

Again it should be emphasized that the bogs give way so gradually to the sedge borders of the ponds on one side and to grassland or heath on the other that areas which we could call true bogs are small in extent as compared with transitional areas difficult to classify.

One reason for the lack of definite boundaries in the bogs was disclosed upon digging below the surface. The sharply limited bogs of temperate regions are commonly developed in distinct depressions filled with peat several feet in thickness. Not so with the bogs on the tundra. Searching for peat

cores for pollen analysis I was unable to find any bog at Katmai underlain by more than a foot of peat. How far the shallowness of the bogs noted at Katmai is characteristic of the region is not altogether clear. Before the eruption there were numerous bogs in the valley of Katmai River and its tributaries, but these were so deeply covered with ash that the thickness of the underlying peat was not determined. At Kodiak within the forest where the rock is a highly contorted slate are many deep ponds fringed with bogs more like those of New England. Some of these bogs rest on beds of peat more than ten feet thick (Bowman, '34).

THE ROCK FACES

At Katmai as elsewhere the vegetation of bare rocks is divisible into lithophytes and chomophytes. The lithophytes, various species of lichens, mostly crustose, play relatively a smaller part than in the high arctic where there is little else by way of plant life. In our region they are of about the same importance as in the vegetation of the temperate zone. They are the pioneers and, theoretically, they assist in the disintegration of the rock surfaces. But practically the activities of the rock lichens are so slow as compared with the rate of change in other stages of the succession that it is hardly appropriate to consider them in the same paper with the rest of the vegetation.

What has been said about the lack of definiteness of the other types of vegetation may be repeated with emphasis as regards the crevice plants, chomophytes. No species peculiar to the cliffs was detected at Katmai. In this matter arctic vegetation is, I am persuaded, less different from temperate than in other respects. Long ago, study in the Sugar Grove area in Ohio (Griggs, '14, pp. 281-287) convinced me that true chomophytes, *i.e.*, plants growing by preference in rock crevices, are few, and that most crevice plants are merely waifs from other habitats whose seed happens to gain lodgment in the crevices. In any particular region, indeed, many of these crevice plants may not be able to compete with the dominant plants in more favorable habitats and so in that area are restricted to the crevices. But an examination of the habitats of such plants in other parts of their ranges usually reveals the fact that their "preference" for the rocks vanishes in areas where competition is less severe.

The nearest approach to a true chomophyte in Alaska is the opposite-leaved saxifrage, whose masses of brilliant purple flowers are especially common high up on the faces of inaccessible cliffs (fig. 9). But in Spitzbergen (Summerhayes and Elton, '23) this plant grows in all sorts of habitats, even acting as a sand binder to fix the miniature dunes which form along the coast.

This view of crevice plants as largely made up of accidental stragglers is, I am aware, at variance with the prevalent European treatment, which regards the chomophytes as a special guild of plants particularly adapted for

this habitat. But while it is perfectly true that many of the crevice plants of the Alps occur nowhere else in that region, an examination of their habitats elsewhere will reveal most of them growing on the ground further north where free from the aggressive competition of the plants of the grassland below the cliffs.

One reason that European ecologists have given so much space to what they consider the special adaptations of chomophytes is that their studies for



FIG. 9. *Saxifraga oppositifolia* in bloom on the scree above the feldmark.

the most part have been confined to regions heavily pastured and so much modified by domestic animals, especially sheep and goats. Ostenfeld ('08) in his account of the vegetation of the Faröes complains again and again of the impossibility of obtaining a real idea of the natural vegetation because of the close grazing and records the surprising fact that the most luxuriant vegetation on those islands is confined to the cliffs and other places inaccessible to sheep. Concerning the crevice plants he remarks, page 984, "A closer examination of these long lists . . . will reveal that only a comparatively

small proportion can be called chomophytes." Most of them belong in other associations.

I am not therefore attempting to give any specific place to the plants of the rocks in describing the vegetation of the Katmai region.

Alkaline Scree, pH 8

Starting from loose rock like the acid feldmark is another succession differing from it in that the rock detritus has a neutral or alkaline reaction which favors a different set of plants.

Long before any other species except occasional waifs can find a foothold on the loose rocks of the talus, *Saxifraga oppositifolia* comes in and grows into strong though isolated clumps which are very conspicuous in their red flowering stage (fig. 9).

The Neutral Feldmark, pH 7-7.5

Below the red saxifrages where loose talus passes into more stable slopes of nearly bare stony ground is the alkaline or neutral feldmark. It is here that the numerous showy-flowered alpine plants so cherished by mountaineers everywhere find their most characteristic development.

In appearance the habitat differs not at all from the acid feldmark, but the difference in reaction excludes the characteristic plants of that habitat. *Empetrum*, *Andromeda*, *Vaccinium*, and other Ericaceae together with *Betula glandulosa* are entirely lacking here.

There is nothing in the feldmark that a pedologist would recognize as a proper soil. The ground is covered with rough angular stones between which is finer detritus still largely unweathered and little changed from the bed rock which lies unbroken a few inches below the surface. The hill is steep and the finer particles wash away rapidly except as they are held by the larger stones or plant roots. Erosion is probably the most important factor in maintaining the habitat in its relatively barren condition (fig. 10).

There is little competition in the feldmark either between the different species or between the individual plants—nothing like a closed vegetation which excludes intruders.

A number of the plants of the feldmark, such as *Silene acaulis*, *Saxifraga bronchialis*, *Polemonium humile*, *Chamaenerion latifolium*, *Campanula langsdorffii*, *Papaver nudicaule*, and others are indifferent to altitude, going down to sea level and even to sea cliffs where there is not too much salt spray. Nevertheless the typical feldmark with the full diversity of its alpine flowers is not to be found, so far as my experience goes, without climbing 1000 feet or more—for reasons which I do not understand.

Comparison of the feldmark with the mixed grassland with which it intergrades has convinced me that there is little special "preference" or adaptation of the species of this situation for their habitat but rather that they are



FIG. 10. Alpine feldmark on the mountain side above Katmai Valley. Altitude about 1000 feet.

plants of slow growth crowded out of the better ground below by more vigorous species and held to a poor habitat where the ordinary grasses and forbs cannot follow them. Any enumeration of feldmark species must therefore be merely a floristic list, so I have arranged the species common there in alphabetical order.

Agrostis hiemalis
Androsace chamaejasme
Anemone narcissiflora
Antennaria monocephala
Arabis ambigua
Arenaria arctica
Arnica lessingii
Artemisia tilesii
Campanula lasiocarpa
Cerastium arcticum
Cerastium vulgatum
Chrysosplenium beringianum
Diapensia lapponica
Draba nivalis
Epilobium latifolium
Euphrasia mollis
Gentiana acuta

Gentiana frigida
Juncoides arcuatum
Konigia islandica
Lagotis glauca
Leontodon sp.
Lloydia scrotina
Myosotis alpestris
Oxytropis campestris var. *coerulea*
Oxytropis podocarpa
Papaver nudicaule
Pedicularis verticillata
Petasites frigida
Phleum alpinum
Poa arctica
Poa glauca
Polemonium humile
Potentilla alaskana

Potentilla villosa
Polygonum viviparum
Primula cuneifolia
Rhododendron camtschaticum
Sagina saginoides
Saxifraga bronchialis
Saxifraga caespitosa
Saxifraga flagellaris
Saxifraga serpyllifolia

Saxifraga unalaschensis
Senecio lugens
Senecio resedifolius
Sibbaldia procumbens
Sieversia rossii
Thalictrum alpinum
Tofieldia coccinea
Trisetum spicatum

MIXED FORB MEADOW

Where the slope is a little less or conditions otherwise more stable so that a soil in the proper sense of the word begins to form, the feldmark gradually gives way to a mixed meadow. The boundary line is quite irregular, with long tongues and patches of meadow penetrating the feldmark in less eroded spots, so that it is easy for one to satisfy himself that the transition is due almost entirely to the development of soil.

Similar mixed grasslands made up entirely of herbs or with a conspicuous admixture of shrubs appear on moderately favorable soils in all the successions. That is to say, mixed grassland is found on the borders not only of feldmark but on heath, bog, dune, and salt marsh as well. Because of its transitions in so many directions and because it has no organic entity but consists merely of weeds which the dominant *Calamagrostis* cannot drive from the poorer habitats as it does from best soils, the mixed meadow is protean in character and impossible to characterize satisfactorily by any reasonable number of species. The following are common but the order of abundance would never be twice the same. Consequently they are set in alphabetical order.

Achillea borealis
Aconitum delphinifolium
Aira caespitosa
Arnica chamissonis
Angelica genuiflexa
Aster sibiricus
Athyrium filix-foemina
Bromus arcticus
Campanula langsdorffii
Campe planisiliqua
Castilleja pallida
Chrysanthemum arcticum
Cypripedium guttatum
Epilobium angustifolium
Equisetum arvense

Festuca altaica
Festuca rubra
Fritillaria camschatcensis
Galium boreale
Gentiana acuta
Geranium erianthum
Heracleum lanatum
Iris setosa
Lathyrus palustris
Myosotis alpestris
Orchis aristata
Polemonium humile
Rhinanthus crista-galli
Salix glauca
Sambucus pubens

Sanguisorba sitchensis
Solidago lipida
Statice arctica
Streptopus amplexifolius
Torresia odorata

Tridentalis europaea arctica
Valeriana capitata
Viola langsдорфii
Veronica wormskjoldii

Among these plants the gray willow, *Salix glauca*, assumes the most conspicuous place, growing up into scrubby bushes a meter tall or less. This is the willow shrub characteristic of many low arctic countries such as south Greenland. It seems to me, however, that the importance of the willows in this association is exaggerated. Like the trees in the poplar forest discussed above, the willows, at Katmai, seem to exert little influence on the other components of the meadow. Writers on Greenland vegetation, such as Warming, and Holttum, agree that the limits of *erect* willows and of grassland are the same. *Salix glauca*, however, goes much further north in Greenland than does grassland, being almost ubiquitous on Disco Island as an espalier in sheltered depressions, i.e., the same degree of severity of climate which prevents the willow from rising off the ground kills off the herbs before they have opportunity to form closed meadows. In Greenland *Salix glauca* is also an important component of heaths and bogs—habitats it avoids entirely with us.

Altogether mixed grassland occupies many hundreds of square miles in the Alaska Peninsula. As one goes northward or westward into more severe conditions where the next association cannot develop it becomes increasingly abundant until over large areas in western and northern Alaska it represents the highest stage of the succession reached.

A meadow very similar to this with about one hundred characteristic species is reported by Hulten, ('27, '32) to be widespread in Kamchatka, which lies 500–1000 miles further south than Katmai and within the limits of forest by an equal distance.

CALAMAGROSTIS-ALNUS ASSOCIATION

Just as the slow-growing alpiners of the feldmark give way before the more vigorous species where soil begins to form, so the numerous weedy species of the mixed meadow are crowded out by the dominant *Calamagrostis scabra*^a in richer soils. On fertile mountain sides this grass, interspersed with clumps of alder, develops into a continuous grassland which has few equals even in the temperate zone. The bluetop here is so deep that a man can scarcely see his way as he plows through it. The average height of the stand is about five feet, but well-grown culms reach seven feet (fig. 11).

Mile on mile along this coast the bluetop-alder grassland stretches unbroken over the mountain sides from sea level to a height of 1000–1500 feet. It is the characteristic plant cover over all the western half of the Kodiak

^a A segregate from the widely distributed *C. canadensis* (Stebbins, '30).

Islands and the southern shore of the Peninsula at least as far west as the Shumagin Islands.

As both the grass and the alder require good drainage for their best growth, the association is confined to well-drained habitats. It is seldom seen on the flats and finds its greatest development on the mountains. Here it thrives on slopes with a steepness scarcely to be matched by other grasslands, attaining full luxuriance in situations that border on the precipitous. Land tilted at 30° – 35° to the horizontal is its favorite habitat and I have observed it in perfect development on a slope which measured 39° by the clinometer.

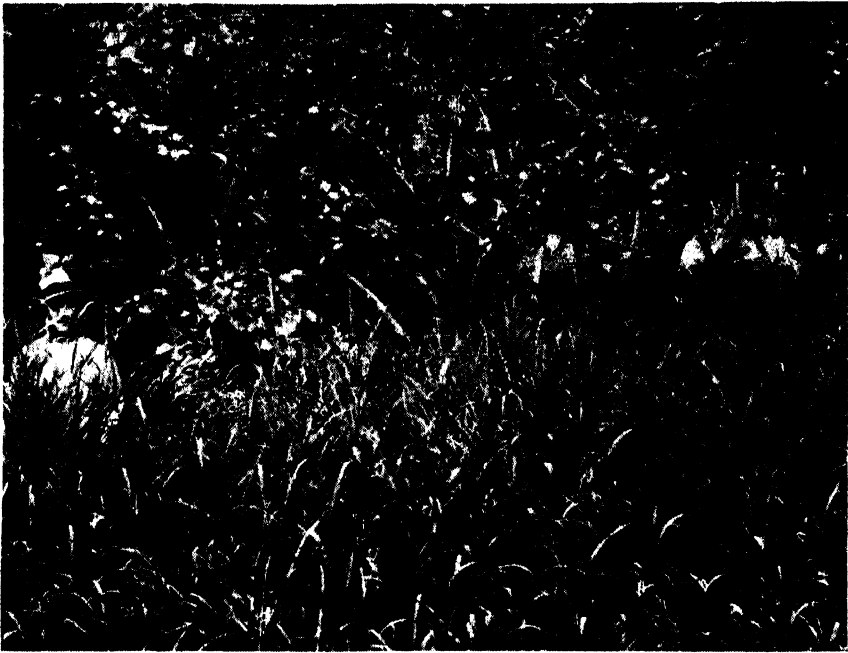


FIG. 11. The *Calamagrostis-Alnus* grassland. The grass often measures seven feet in height and is so thick as to keep out all competitors including seedling alders. The man standing in the grass is six feet tall.

Climbing mountains covered with this grass is hard work, although the grass gives good handholds to compensate for its slipperiness underfoot. But sliding down is great sport comparable only with sliding down steep snow fields in other places. One may sometimes cast loose on a smooth, unbroken slope and slide down as on a toboggan for hundreds of feet before any obstruction arises to stop progress. At Kodiak where the natives cut the blue-top hay for their cattle, it is the custom to gather up a ball of it into a fish net, give it a kick and send it rolling and bounding into the valley below.

In contrast with nearly all the other types of vegetation in our area, the description of this, the climax or permanent subclimax, is simplicity itself. In the typical association there are only two species, *Calamagrostis scabra* and *Alnus sinuata*.

But there are, of course, all possible transitions from the mixed meadow to the pure grassland in proportion as there are richer and poorer spots in any soil. The meadow species which survive longest are, naturally, those of the strongest growth most able to compete with the grass. Thus a whole mountainside, otherwise a pure stand of grass and alder, may be dotted here and there with individual plants of the rank umbellifers, *Angelica genuiflexa* and *Heracleum lanatum*.

The interrelations of the two dominant species, grass and alder, were not determined with complete certainty. Each aggressively extends its occupancy wherever opportunity offers, but their powers of competition and of holding on are so nearly the same that neither makes much headway against the other.

Outside their association the two components manifest somewhat different habits. The alder is exclusively a plant of well-drained habitats, especially characteristic of new stony ground, particularly on the higher slopes. It grows in crevices in the rocks of the feldmark. Small hollows in the rocks such as fill with snow in the winter are commonly occupied by an alder of espalier form whose branches fill the depression with a thick mat of twigs up to the general level, though they do not extend above the surface of the snow where they would be exposed to the force of winter storms. It is likewise a typical pioneer on alluvial cones where the ground is largely coarse rock detritus rather than true soil. Further south where snow slides are common it is regularly a pioneer in avalanche tracks.

Calamagrostis scabra, on the other hand, is almost ubiquitous. It is found in most of the habitats of the region. It will crowd into the edges of tide flats, constantly inundated (though by fresh rather than by salt water). It is usually to be found in the bogs. On the heath it is more abundant than any other grass or sedge. It is the characteristic pioneer on secondary ash deposits. In all these habitats, however, its growth is relatively poor. Its best development occurs only in the deepest and richest soils.

When alder and grass come together on the fertile hillsides their powers of growth are so evenly balanced that they will live together for many years, and perhaps indefinitely, without either gaining the upper hand. Each perpetuates itself and spreads vegetatively, so that no question of their relative life-spans enters in as would be the case if a long-lived tree were competing with a short-lived herb. The grass forms a heavy turf of interlacing roots and stems so that it is renewed each year. The branches of the alder lop over onto the ground and take root with age, forming sprawling clumps, the peripheral portions of which are always young.

Yet it seems to me that the grass is somewhat the stronger of the two. It grows vigorously under the shade of the alder—almost as vigorously as in the open (fig. 11). It is the close-set culms of the grass rather than the sprawling trunks of the alder which exclude other plants. For on alluvial cones and other new ground an abundance of other species comes up under the alders.

Further, it is doubtful whether the alder, once eliminated, could regain its place. At least it did not come back in eighteen years where killed by the eruption. Along the mountain slopes southwest of Katmai there is an area of twenty or thirty square miles which, though swept by blasts from the volcano that killed all trees and bushes, did not receive a heavy coating of ash. In this area the grass promptly came up from the uninjured roots. But the alders have not come back and no seedlings were observed in the grassland, though abundant seed is produced nearby in areas protected from the blast.

Again, it would hardly be possible for the deep rich humus soil characteristic of the association to develop under alders alone. Very few types of plant cover, indeed, could hold and build up a soil on a 30° slope. But the long culms of the grass lop down under the winter snow and form a thick thatch which effectually prevents erosion.

Year after year a large amount of organic matter is thus laid down on the ground. Each layer is held in place by its attachment to the roots until the next season's growth comes down on top of it. The decay of the matted grass thus adds leaf mold to the ground until, despite the slope, a very thick and rich humus soil is built up. Pits dug in a grassland gave interesting information concerning the soil.

One of these soil pits which revealed typical conditions was dug on a hillside about ten feet from the edge of a steep gully in which, at a lower level, an alder was growing. The side slope back from the edge of the gully on a line perpendicular to the main slope was about 1 to 10, the main slope about 1 to 3. The section showed:

	Thickness	Total
New humus and duff	2 inches	
Katmai ash	4 "	6 inches
Dark-brown humus loam, pH 5-5.5	18 "	24 "
Shading into lighter-brown humus loam	12 "	36 "
Yellowish-brown sandy loam, pH 5.5	36 "	72 "

On the bottom of the pits were found a few loose stones but no certain indications of the sandstone bed rock which, however, could not have been far beneath as judged by outcropping ledges in the adjacent gully. The upper foot was occupied by closely matted grass roots. The second foot had about one-third as many roots as the first. The third had again about one-third as many as the second and a few, perhaps again one-third of those above, penetrated into the fourth foot. There were also a number of roots from the adjoining alder in the gully. These were almost all about one foot below the surface. A few of them were as much as eighteen inches down but none below that point. As these roots were higher than the base of the trunk, they had followed uphill around the contour of the ground, keeping close to the surface. Their distribution was thus not at all controlled by the supply of plant food in the soil but depended presumably on oxygen-moisture relations.

GRASSLAND NOT A TRUE CLIMAX

Developing from the mixed meadow, the bluetop-alder grassland is clearly the culmination of the succession in the Katmai district. Nevertheless, there is good reason to doubt that it is the highest vegetation type that the climate of the area would support. That is to say, it is not a true climax.

Doubt of the climax character of the grassland rests on two sets of facts: First, as pointed out in the introduction, the advancing border of the forest, which forms the inner boundary of our region, is not at all a climatic line and this of itself forbids any conception of the grassland as a true climatic climax.

The details of the evidence of this forest advance (Griggs, '34; Bowman, '34) cannot be repeated here but may be summarized by the statements that: (1) The trees at the forest edge are all young; (2) the forest has made a marked advance since its position was first described in the 18th century; and (3) the study of fossil pollens preserved in the bogs gives no evidence of a nearby forest since the glacial period.

How much further the migration of the forest is destined to go no man can tell. But to the Shumagin Islands no climatic barrier is apparent. Indeed, a few Sitka spruces planted in 1805 by the Russians at Unalaska, 600 miles beyond the edge of their natural boundary, are still flourishing (fig. 12).



FIG. 12. Sitka spruce at Unalaska, 600 miles beyond its natural boundary. These trees were planted in 1805 and while they bear cones the seedlings would have scant chance against the goats.

Fernow ('02) reported: "At the time of our visit the largest measured 24 inches, the smallest 6 inches, in diameter, while all were the same height, 25 to 30 feet. The trees had been fruiting heavily the year before, and two smaller ones at a distance were undoubtedly the result of an earlier seed year." According to R. S. Capps (personal communication) they produced a copious crop of cones in 1932, yet the original planted individuals have not multiplied.

The apparent absence of seedlings is, however, not very significant in view of the fact that the island has now for many years been overrun by goats, which, as is well known, destroy coniferous seedlings as fast as they come up. The success of spruces at Unalaska is in marked contrast to an attempt to grow spruces in southern Greenland reported by Holttum ('22, p. 104), "It is interesting to note that seeds of *Picea excelsa* were sown in Agdluitsak fjord ($60^{\circ} 30' N.$) in 1846 and in 1886 three specimens collected had only reached one meter in height."

Second, the *Calamagrostis-Alnus* grassland is an anomaly among arctic plant societies. Nowhere else in the arctic, so far as I have been able to ascertain, is grassland of similar type or of comparable luxuriance to be found. All other arctic grasslands are a very mixed assemblage with many species of forbs and sedges as well as grasses, *i.e.*, like the mixed meadow described above. Back in the Hudsonian zone, however, such *Calamagrostis* grassland, with or without the alders, is characteristic of openings in the forest. Thus in Alaska it is widespread through much of the interior.

West of Edmonton, Alberta, near the *southern* edge of the southern division of the subarctic forest where it joins the prairie are extensive tracts of practically identical meadow, here *Calamagrostis canadensis*, typical, which are cut for hay with no more improvement than in Alaska. I have a photograph taken in 1935 which gives practically the same picture as that shown in figure 13. From this region such meadows extend for a long distance northward

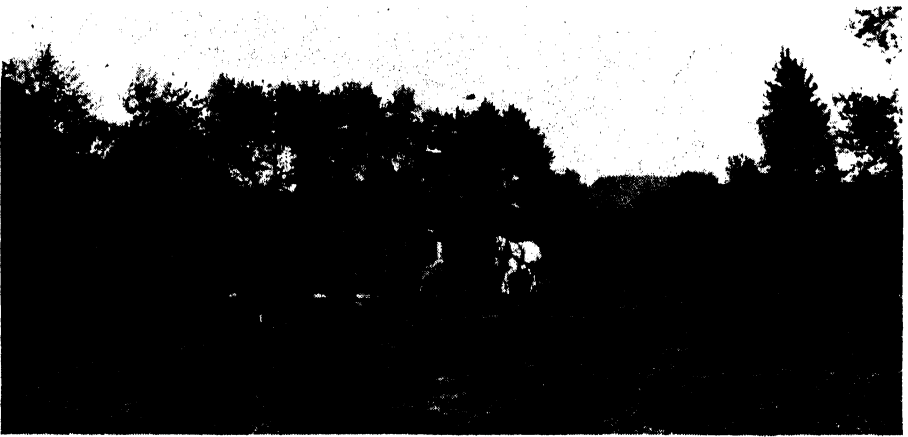


FIG. 13. A *Calamagrostis* meadow on Kodiak Island. Nothing has been done to improve the stand of grass for haying purposes except to cut the scrub alders, willows and poplars. The trees are balsam poplar. Photo by D. B. Church.

toward the arctic. Porsild ('29, p. 43) figures one at Fort Franklin on the Mackenzie.

A similar grassland composed of *Alnus fruticosa* and *Calamagrostis langsdorfii*, which is regarded by Hulten ('28) as conspecific with *Calamagrostis scabra* (Stebbins, '30), is said to occupy large areas in subarctic Kamchatka.

SHOULD AN AREA WITH A SUBARCTIC CLIMAX BE CLASSIFIED AS ARCTIC?

The fact that the "climax" vegetation is thus subarctic rather than arctic brings us back to the problem considered briefly in the introduction. Is not our area after all subarctic (Hudsonian), rather than arctic? Since the "climax" is Hudsonian it might appear logical to classify the whole area in that zone. But when it is recalled that grassland is never the climax in the Hudsonian, it is clear that such a procedure would be entirely untenable. Again, though from some points of view it might seem desirable to classify all territory climatically suitable for forest as Hudsonian, practically we are far from possessing sufficient understanding of the factors controlling forest limits to do so.

If we could determine the point where the advance of the forest would ultimately come to a halt, we could have no assurance that it would not shift under secular changes of climate before the migrating trees caught up to it. If we attempted such a thing, we should be laying down a theoretical line which would be of no use to anyone in the field. For, while the edge of the forest is one of the clearest of vegetation lines, the transition from the bluetop-alder grassland to the mixed meadow, which would become the outer limit of the arctic if the forest border is discarded, is everywhere most gradual and indefinite. Further, as has been said before, the mere presence of the trees introduces so many changes into the conditions of life not only for both plants and animals but for soil formation as well that the forest border must be recognized as of major ecological significance even though timber line be a shifting dynamic boundary rather than a static limit.

It may seem very unsatisfactory to be unable to correlate our vegetation zones with climatic factors, but it should be remembered that stable climatic limits are approached only when climatic and geological changes are at a standstill. We know very well that throughout the geological past vast changes in climatic conditions were constantly in progress. There is no reason whatever for supposing that they have ceased. Until recently we have had no idea of the rate at which they were occurring. But now findings in several fields are beginning to tie in the geologically recent past with the present. I refer to the study of varved clays, of tree rings, and of fossil pollens. To the significant advances in these fields, ecological study is capable of yielding important assistance. But if we are to begin to work out ecological interpretations of geological changes we must give up our ideas of a static ecology wherein animals and plants are assumed to be closely adjusted to the conditions of a stable environment and examine nature with an open mind to see whether there are not other cases like the present where biota are in process of active adjustment to a changing environment.

The place to begin such study is at the termini of the ranges of plants and animals. Study at such a place, as was pointed out long ago by the writer (Griggs, '14b), can tell us with great precision, as it has at Kodiak,

whether a species is gaining or losing, advancing or retreating. And a series of such studies can give us the trends of climatic change. Such surely is a goal worthy of the effort involved in its pursuit.

SUMMARY

The Katmai district lies just beyond the limit of coniferous forest in southwestern Alaska. For hundreds of miles along the Alaska Peninsula and on the western half of Kodiak Island the best habitats are occupied by a grassland composed of *Calamagrostis scabra* in practically pure stand except for clumps of *Alnus sinuata*. This grassland is especially at home on mountain sides, where, despite the steepness of the slope, which may exceed 30°, the grass has built up a deep humus soil which, where excavated, is full of sandy humus (not peat) for a depth of two meters. The grass grows six or seven feet tall and forms a heavy turf which excludes all other plants except the alder.

The *Calamagrostis* grassland belongs not with the arctic vegetation of other habitats but back in openings in the Hudsonian spruce forest which here has not reached its climatic limit but is advancing, i.e., the grassland is the forerunner of forest and occupies habitats suitable for trees.

Except for specialized habitats like dune and salt marsh, the *Calamagrostis-Alnus* grassland is the only true "association" in the region, i.e., a vegetation type whose composition is determined by competition. The rest of the vegetation is typically arctic, miscellaneous in composition, never twice the same, without definitive "character species" and the various types run together inextricably. The two most widespread types are (1) a mixed meadow with half a hundred species on soil too thin for the domination of *Calamagrostis* and (2) a dwarf shrub heath in which *Empetrum* is the most abundant plant in poorly drained situations. The surface of the heath has grown into a remarkable alternation of bare or nearly bare hollows and steep-sided, heavily vegetated ridges which sometimes exceed a meter in height.

In a general way the description of the vegetation at Katmai will cover a large part of interior and western Alaska.

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A COMPARATIVE STUDY OF THE ABUNDANCE AND THE RATE OF GROWTH OF *MYA ARENARIA* L. IN THE GULF OF ST. LAWRENCE AND BAY OF FUNDY REGIONS¹

CURTIS L. NEWCOMBE

University of Maryland

INTRODUCTION

This paper deals with variations in abundance and rates of growth of *Mya arenaria* L. occurring in areas not far removed from each other, yet possessing significant ecological differences. In the Gulf of St. Lawrence region, the clam beach selected for intensive study is located on the south shore of the Gulf about two miles above the mouth of the Bideford River. The Bay of Fundy experiments were conducted at Clam Cove, Deer Island, situated near the mouth of the Bay.

In comparing the two regions, consideration was given to certain environmental factors (Newcombe '35c), such as beach soil, food, water temperature, salinity; to the relative abundance of *Mya* at several intertidal levels, including relative abundance of different length classes at each level; and to seasonal as well as annual growth rates for "small" and "large" specimens. On a basis of comparable growth experiments, it has been possible not only to establish differential growth rates for the two regions, but to throw some light on the relative importance of certain environmental factors in affecting the extent of growth.

DESCRIPTION OF BEACHES

The beach studied in the Bideford River possesses an intertidal zone approximately ten meters in width. The rise and fall of tide is approximately three feet, hence there is relatively little water movement over the beach. The current, apart from the drift caused by oblique waves, is seldom perceptible along the shore. The area populated by *Mya arenaria* extends shoreward to a distance of about six meters above the mean low water level, the equivalent of a perpendicular tidal amplitude of 1.5 feet. The Clam Cove beach possesses a gradual slope, as indicated by the fact that the distance between mean high and low water levels is about four hundred meters, the tidal amplitude being approximately twenty feet.

Sand is the characteristic soil type of the Bideford beach, whereas at

¹ Contribution from the Zoological Laboratories of the University of Toronto and the Johns Hopkins University.

Clam Cove the soil consists of a mixture of sand and mud, the former predominating at the upper levels and the latter at the lower zone of the beach.

From a standpoint of growth no important differences in salinity have been found, the range being from about 28 to 32 per mille.

Significant temperature differences exist in the regions of study (Newcombe, '35c). Comparing the monthly water temperatures of the two regions, it was found that: (1) mean water temperatures in Prince Edward Island waters during the period, May 1 to October 1, 1932, are higher, (2) very similar mean water temperatures obtain during October, and (3) water temperatures in the Clam Cove area are higher during the period from November 1 to about April 15 (Newcombe, '35b). In the Prince Edward Island region there is a much more pronounced rise in the spring and drop in the fall temperatures. During 1931, the water temperature of the Bideford River remained at or below 0° C. until April 6, by April 20 it had risen to 5.3° C. and on May 2 it registered 8° C. The highest mean monthly temperature, 21.8° C., for the Bideford River in 1932 was reached in August, and that for the Clam Cove area, 13.1° C., was also during August. In the Prince Edward Island waters the most pronounced drop in temperature occurs during November. In 1932 the mean water temperature from November 1 to November 23 was 4.2° C., whereas from the 24th to the 30th, the corresponding mean value was 0.4° C. Thus, the mean temperature for the month, 3.4° C., is significantly less than that for the Clam Cove area (8.6° C.) (Newcombe, '35a). The mean water temperature at Bideford River, during the "summer" period (June 13–August 28), was 20.5° C., as compared with 11.4° C. in the Clam Cove region (table I).

TABLE I. *Seasons, their duration and temperatures during experiments of 1931 and 1932 in the region of Clam Cove, N. B.²*

Seasons	Duration of Seasons	Number of Days	1931		1932	
			Mean Daily Temperature Water °C.	Air °C.	Mean Daily Temperature Water °C.	Air °C.
"Spring"	March 1 to June 19	111	4.97	6.95	3.57	4.04
Total period						
Growth period	May 1 to June 19	50	7.62	8.04	7.19	10.59
"Summer"	June 20 to August 17	59	12.11	17.97	11.45	16.81
"Fall"	August 18 to October 14	57	12.31	13.64	12.83	13.99
"Late Fall"	October 15 to December 3	50	9.06	6.30	—	—

² Seasonal mean water temperatures represent the mean of daily mean temperatures based on the average of two readings taken about 8 A.M. and 5 P.M. Mean air temperatures represent the mean of daily mean temperatures obtained by calculating the mean of the maximum and minimum daily temperatures.

Food

In the absence of quantitative plankton data, stomach analyses were made for comparative purposes. Similar results were obtained for the two regions. Certain diatoms—*Navicula*, *Pleurosigma*, and *Paralia*—were common, and among the zooplankters, certain tintinnids such as *Tintinnus subulatus* and *Tintinnopsis campanula* predominated.

POPULATION OF BEACHES

Bideford River, Prince Edward Island

For population comparisons, four stations were selected for quantitative sampling at levels of about 2.4, 2.7, 3.1, and 3.6 feet above chart datum. Observations were made during the early part of June, 1932, and it was found that near the mean high water level, about 3.6 feet above chart datum, there was a total absence of clams other than the set of 1931. The specimens ranged from 4 mm.—12 mm. in length and numbered as high as 700 per meter square area. Results indicate that there was a late set in 1931, since the examination of gonads³ collected weekly after May 5 showed that extensive spawning had not started by this date (June 12). At the lower levels the average number of small clams (4 mm.—20 mm. long, 1931 set) obtained was 300 per meter square area, the most abundant sizes ranging from 5 mm. to 8 mm. in length. The number of clams over 20 mm. in length at a 2.7 foot level ranged from about 200 to 300 per meter square area, thus representing a population similar to that of the Bay of Fundy region.

Population analysis has shown that about 63 per cent fall within the range 45 mm.—64 mm. and that the number above 84 mm. in length is relatively insignificant (table II). These data are essentially in agreement with the Bay of Fundy findings. Results of experimental growth in nature warrant the suggestion that the length class 15 mm.—24 mm. represents 1931 set.

TABLE II. *Relative abundance of Mya arenaria in each length class at a low level on the beaches at Bideford River, Prince Edward Island, and Clam Cove, N. B.*

Length Class in Mm.	Percentage	
	Bideford River	Clam Cove
15-24	9.0	7.1
25-34	2.3	7.8
35-44	6.3	22.0
45-54	32.4	35.7
55-64	30.6	19.8
65-74	11.3	2.7
75-84	6.7	
85-94	1.4	

³ For assistance in recognizing the various stages of gonadal development, the writer is most grateful to Dr. Alfreda Berkeley Needler of the Prince Edward Island Biological Station.

The date at which set first appear is not known. Observations indicate that extensive spawning does not take place before June 12 (1932). Dr. Needler⁴ states that in 1932 large numbers of small clams, from one to two mm. in length, were observed on shells in this locality, the number in some instances being as high as 100 per shell. These were first noticed on July 1st of that year. It seems probable, therefore, that the settling of the clam larvae occurred about the middle of June. Two experimental boxes planted in June 1933 contained 122 small clams, ranging in size from 8.0 mm. to 17.0 mm. when removed in November. The distribution of length classes was as follows: 8.0 mm.-10.9 mm., 41 per cent; 11.0 mm.-13.9 mm., 44 per cent; 14.0 mm.-16.9 mm., 14 per cent. The mean lengths of the groups from the two boxes were 11.8 mm. (N=74) and 11.3 mm. (N=48). These results seem to give a fairly reliable expression of the extent of growth during the first year. Doubtless these values vary considerably from year to year since the effect of seasonal variations on growth is likely to be most pronounced at this stage of development.

Clam Cove, New Brunswick

In the Bay of Fundy region clams are found in greatest numbers at or below the half tide level. The population is characterized by a wide range of length classes, with the dominant classes ranging from 35.0 mm.-64.0 mm. The most prominent length class, however, is 45.0 mm.-54.0 mm. The numbers of specimens per meter square area at levels 16, 13, 11, 9, and 7 feet above chart datum are 27, 240, 372, 362 and 72 respectively (fig. 1B). Small clams (3-34 mm. in length) are concentrated at the upper levels (16 feet), the dominant length class at this level being 25 to 34 mm. Specimens above 54 mm. in length rarely occur at this level on the flats. At levels 11-13 feet the dominant length class has shifted to 45-54 mm. and the classes 35-44 mm. and 55-64 mm. are very prominent. At levels of 7-9 feet there is evidently a quite similar distribution of length classes, the same dominant class occurring as at levels 11-13 feet. The larger classes, especially the 65-74 mm. class, may be influenced by digging operations carried on each year at this beach. It is not improbable that the results presented for the length class 5-14 mm. are somewhat erratic, due to unsatisfactory methods for locating very small clams in mud soil. Figures are not presented for levels below seven feet owing to the fact that only an occasional specimen is present (fig. 1). The marked reduction at the low levels is due to the presence of a layer of silt on the surface of the beach (Newcombe '35b, '35c).

Surveying the data collected it is seen that the total clam population per unit area at a low level in the Clam Cove region is considerably less than in the Bideford area, and the vertical distribution far more extensive.

⁴ Personal communication.

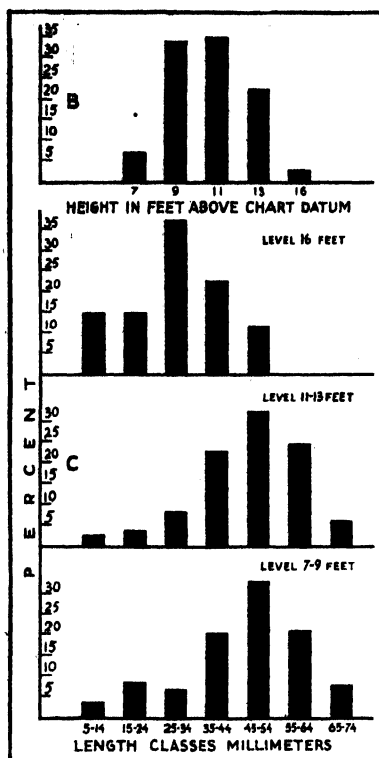


FIG. 1. B. Abundance of *Mya* expressed in per cent at different levels on the intertidal zone at Clam Cove, N. B. C. Relative abundance of different length classes of *Mya* at three levels on the beach at Clam Cove, N. B., expressed as a percentage of the total for each level. Percentages for levels 11 and 13 feet and for levels 7 and 9 feet have been averaged.

EXTENT OF GROWTH

Growth experiments were conducted throughout 1931 and in 1932, during the periods designated "summer" (June 13th to August 28th—75 days) and "fall" (August 29th to October 20th—53 days). In the Bideford River area, the 1933 experiments were set up on May 20th and terminated November 15th (179 days), a period, which, it is believed, includes the entire growing season.

Bideford River, Prince Edward Island

During the "summer" period, 1932, clams possessing an initial length of 22.8 mm. (level 2.7 feet—low) exhibited an absolute increment of 8.1 mm. (percentage addition—35.7). Specimens having an initial length of 33.1 mm. showed an absolute increment of 6.1 mm. (18.3 per cent) indicating a marked reduction in growth rate accompanying an increase in initial length of 10.3 mm. The extent of growth during the "fall" period was quite similar to the "summer" increment, being significantly greater than that occurring in the Bay of Fundy region (table III). On a basis of temperature

TABLE III. *Growth during the "summer" and "fall" seasons of 1932 at Biddeford River, P. E. I., compared with that at Clam Cove, N. B.*

Location	Season	Initial Length in Mm.	Absolute Increment of Growth in Mm.	Percentage Addition of Length
Biddeford R.	"Summer"	33.1	6.1	18.3
Clam Cove	"Summer"	34.1	2.9	8.6
Biddeford R.	"Fall"	30.4	7.8	25.5
Biddeford R.	"Fall"	39.2	4.1	10.5
Biddeford R.	"Summer"	22.8	8.1	35.7
Clam Cove	"Summer"	22.7	4.0	17.7

data, it may be concluded that little, if any, growth takes place after the end of the "fall" period (October 20th) or prior to April 20th. Data pertaining to the amount of growth before June 13th, 1932, ("spring" period) are not available.

The growth data for 1932 contribute toward a more satisfactory understanding of the "annual" extent of growth characteristic of the latitude in question (table IV). Comparing these results with those for the preceding

TABLE IV. *Annual growth of Mya arenaria in the Biddeford River and Clam Cove Areas*

Location	Number of Specimens	Initial Mean Length in Mm.	Absolute Growth Increment	Percentage Growth Increment
Clam Cove	45	18.5	12.1	65.3
Clam Cove	45	22.4	10.1	45.1
Biddeford R.	43	22.8	19.9	87.2
Clam Cove	45	26.6	8.2	30.7
Biddeford R.	38	30.4	18.6	61.1

"summer" and "fall" periods, referred to above, a general idea of the extent of growth during the "spring" season is obtained. It is clear that the extent of growth in this region is significantly greater than that occurring in the Bay of Fundy region (tables III, IV and VI).

Clam Cove, New Brunswick

Growth experiments on the Clam Cove beach were set up during the period from February 26th to March 3rd, 1931, and the four succeeding periods of measurement were June 18-26, August 14-18, October 13-18, and December 3-8, 1931. The intervals between these five periods of measurements have been designated "spring" (111 days), "summer" (59 days), "fall" (57 days) and "late fall" (50 days). Measurements made during the period December 3-8, 1931, indicate that no appreciable growth took place during the "late fall" period, hence it can be assumed that practically no growth occurred between the middle of October and the first of March.

An expression of the "annual" increment of growth has been obtained by summing the increments during the "spring," "summer" and "fall" periods

(March 1 to about the middle of October). These yearly values are probably somewhat less than the true increments on account of the retardation in growth rate caused by the clams being disturbed for the purpose of measurement. The "annual" increment obtained for clams possessing an initial mean length of 18.5 mm. was 12.1 mm. (65.3 per cent) and for specimens having an initial length of 26.6 mm., the corresponding increment was 8.2 mm. (30.7 per cent). A comparison of the seasonal growth of "small" and "large" clams at the same level (7 feet above chart datum) is presented in table V. It is seen that the "spring" and "summer" increments of the larger group are approximately the same whereas the small clams show a somewhat larger percentage addition of length (30.0 per cent) during the "summer" season. The absolute increment of growth during the "fall" period is below 1 mm. in both size groups. The seasonal growth rates for 1932 are presented in table III.

TABLE V. Seasonal growth expressed in mm. during 1931 at Clam Cove, N. B.

Seasons	Average Length at End of Each Season	Seasonal Absolute Growth Increment	Seasonal % Length Addition	Average Length at End of Each Season	Seasonal Absolute Growth Increment	Seasonal % Length Addition
Box A—Level 18 Feet			Box B—Level 7 Feet			
Initial Length—18.4 mm.						
"Spring"	20.1	1.8	9.7	22.8	4.3	23.5
"Summer"	22.9	2.7	13.4	29.7	6.9	30.0
"Fall"	23.9	1.0	4.5	30.5	0.9	2.9
Total		5.5	30.0		12.1	65.3
Box A-1—Level 18 Feet			Box B-1—Level 7 Feet			
Initial Length—26.4 mm.						
"Spring"	28.9	2.5	9.6	30.2	3.7	13.7
"Summer"	20.9	1.9	6.6	34.3	4.1	13.5
"Fall"	31.7	0.8	2.7	34.8	0.4	1.3
Total		5.3	20.0		8.2	30.7

TABLE VI. Constants of frequency distributions of lengths of *Mya arenaria* L. employed in growth experiments

Time	Locality	Initial Mean Length in mm.	Standard Deviation	Final Absolute Length in mm.	Standard Deviation
"Summer"	Clam Cove	22.7±0.1	1.02±0.07	26.7±0.3	2.51±0.18
"Summer"	Clam Cove	34.1±0.1	1.21±0.09	37.1±0.3	2.65±0.20
"Summer"	Bideford R.	22.8±0.1	1.13±0.08	30.9±0.2	2.47±0.18
"Summer"	Bideford R.	33.1±0.1	1.20±0.08	39.2±0.3	2.71±0.20
"Fall"	Bideford R.	30.4±0.1	1.15±0.08	38.2±0.2	2.45±0.18
"Fall"	Bideford R.	39.2±0.1	1.22±0.09	43.3±0.2	2.31±0.17
1931	Clam Cove	18.4±0.1	1.04±0.11	23.9±0.2	1.31±0.13
1931	Clam Cove	18.5±0.1	0.96±0.10	30.5±0.4	2.45±0.26
1931	Clam Cove	26.4±0.1	0.84±0.08	31.7±0.2	1.60±0.17
1931	Clam Cove	26.6±0.1	0.97±0.10	34.7±0.4	2.77±0.30
1932	Clam Cove	22.4±0.1	0.96±0.07	32.5±0.2	1.85±0.14
1932	Bideford R.	22.8±0.1	0.98±0.07	42.7±0.2	1.66±0.12
1932	Bideford R.	30.4±0.1	1.11±0.09	49.0±0.2	1.85±0.14

DISCUSSION

Clam populations are known to lack stability due to natural causes (Weymouth, '23). Periodicities in respect to annual abundance of set probably occur in both the Gulf of St. Lawrence and the Bay of Fundy regions. A relatively high peak is known to have occurred in the Bay of Fundy during 1932, when numbers of set as high as 6000 per meter square area were recorded. During this season, large numbers were also reported in the Bideford River but unfortunately no previous or subsequent records are available which might suggest the length of the cycle. A comparison of the populations on the two beaches under consideration has shown that in both areas, the dominant length classes range from 35 mm. to 65 mm. This concurrence obtains in spite of the marked differential growth rate reported from this study. Significantly greater numbers of small clams below 14 mm. in length characterize the Bideford River area. Furthermore, extensive sampling on practically all the clam beaches of the Bay of Fundy showed that clams above 75 mm. in length are very scarce, an additional point of difference. The character of the distribution of length classes in the two regions shown in table II and the occurrence of a significantly faster rate of growth in the P. E. I. region would seem to indicate an explanation not found in natural phenomena. The cause may lie in the extensive commercial digging in the Bay of Fundy region, thus not permitting a definite deduction pertaining to differential longevity or to a possible difference in maximum size attained in the two regions. In the absence of any digging, there would presumably be more large and therefore older clams at Clam Cove. It has been shown that here growth is slower than in the Bideford River and that the size distribution is quite similar. From these observations, a greater longevity at Clam Cove may be deduced and the fact of digging strengthens that conclusion. It seems quite safe, therefore, to conclude that the growth rate is faster and the longevity less at Bideford River.

Comparison of our results with those of Belding ('16) for the Cape Cod region shows that in colder waters *Mya arenaria* attains a greater age (Newcombe, '35c), and grows at a lower rate. The amount of set is also less. It appears that the Bideford River area occupies an intermediate position between the Cape Cod and Bay of Fundy regions (Compare Newcombe '36 and Newcombe and Kessler '36). In this connection, Weymouth, McMillan and Rich ('31) who studied the growth rate of *Siliqua patula* at widely different latitudes on the Pacific Coast, state "in the south the rate of growth is rapid; the life, short; and the set, heavy. In the north the rate is low; the life, long; and the set, light."

In discussing the distribution of the length classes of clams on the intertidal zone, the results presented in figure 1-B and C, which shows the abundance of each length class at several levels, may be compared with the facts pertaining to growth rate at approximately corresponding levels.

Attention is given to the probable reasons for the concentration of the total population (90.8 per cent) between levels 9 and 13 feet above chart datum. Observations on numerous beaches indicate that slope together with current (inseparable factors) largely determines the concentration at upper levels, *e.g.* a beach near Upper Clements, N. S., where the number present is about 855 per meter square area. In the case of a beach possessing a very gradual slope, a more regular and uniform set is expected, *e.g.* Clam Cove. Other factors being equal, it seems reasonable to expect a gradual increase in the direction toward low water level on account of the greater time of submergence for deposition of set to occur. If this were true, the occurrence of such phenomena would be prevented at Clam Cove on account of the soft mud and a surface layer of silt at the very low levels which limit the survival of the set, hence, the abundance at the levels 9 to 13 feet. Whether or not this is the true explanation, it is obvious that currents, shore slope, and soil must constitute dominant controlling factors.

Considering the abundance of each length class as illustrated in figure 1, it is seen that (1) the larger percentage of small clams is present at a high level, (2) below eleven feet the dominant length classes range from 35 to 64 mm. These results are due largely to a higher rate of growth at the low levels. The high percentage of small clams present at the sixteen foot level might be caused by a heavier set at this level. However, a determination of the age of the population shows clearly that this is simply a reflection of the comparatively slow growth which we have confirmed by experiment at high levels (Newcombe, '35c). The dominant length classes occurring below eleven feet at Clam Cove correspond with those of the entire Bay of Fundy and may be correlated with climatic conditions.

The complexity of factors operating in nature which determine the growth rate of this species renders a definite explanation of variations obtained very difficult. Comparable experiments carried on during the "summer" season of 1931 and during the entire growing season of 1932 have shown that the rate of growth in the Bay of Fundy region (Clam Cove) is approximately one-half that of the Bideford River area (table IV). In the Bay of Fundy, the seasons of greatest growth are "spring" and "summer" with a pronounced decrease during the "fall" period. These seasonal differences have been correlated with variations in the abundance of food rather than temperature. During the growth period of the "spring" season (May 1 to June 19), the mean water temperature was 7.62° C. in comparison with 12.31° C. for the "fall" period when very little growth occurred. It is believed that in the Bay of Fundy waters food rather than temperature is the factor of most direct importance (Newcombe, '35c).

In an attempt to explain the higher growth rate which characterizes the Gulf of St. Lawrence region, salinity, circulation, food and temperature are considered. The salt content is essentially the same. Water circulation,

however, is much greater in the Bay of Fundy where the growth rate is slower.

With respect to the food factor, examination of stomach contents of over 300 clams collected from the Bideford River beach on June 12 and August 28, 1932, indicated a dominance of *Pleurosigma*, *Paralia* and certain colorless flagellates. These findings correspond quite closely to the results obtained in the Bay of Fundy samples. Unfortunately qualitative and quantitative data pertaining to the plankton of this region are not available for comparison. On a basis of our knowledge of the relative importance of the several environmental factors affecting the growth of *Mya arenaria*, it seems likely that the higher mean temperature of about 9° C. (table I) which may be reflected in the quantity of food, constitutes the explanation for greater growth in the Gulf of St. Lawrence waters. This conclusion has been reached in spite of the fact that in the Bay of Fundy region seasonal differences in rate of growth were correlated with variations in the amount of food and not temperature *per se*.

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SUMMARY

1. The part of the intertidal zone of the Bideford River populated by *Mya arenaria* extends toward the shore for a distance of about 6 meters from the mean low water level equivalent to a perpendicular tidal amplitude of 1.5 feet as compared with a distance of approximately 300 meters and a corresponding amplitude of 18 feet in the Bay of Fundy area.

2. The population of *Mya arenaria* on the beach at Clam Cove, N. B. (Bay of Fundy) is characterized by (a) paucity of small clams representing set of 1928, 1929 and 1930, (b) dominant length classes ranging from 35 to 65 mm. On a basis of our knowledge of the growth rate in this region, the dominant length classes seem to reflect favorable climatic conditions for survival of set during the four years 1924–1927.

3. The population (above 20 mm. in length) at Clam Cove varies widely according to the beach level, there being, as a rule, a more numerous population at levels extending from nine to thirteen feet above chart datum with a noticeable decrease above and below these levels. Numbers varying between 250 and 350 per meter square area frequently obtain.

4. In the Bideford River, Gulf of St. Lawrence, the clam population (apart from the set of 1931) numbers between 200 and 300 per meter square

area. The range of dominant length classes (45 to 65 mm.) is similar to that of the Clam Cove beach. However, the numbers of small specimens (below 20 mm. in length) were, during the periods of study, significantly greater in the warmer waters of the Gulf of St. Lawrence.

5. "Small" clams (18.5 mm. in length) exhibit a faster rate of growth than large individuals, 26.6 mm. long, throughout each season at Clam Cove, N. B., the annual absolute increment of growth for small clams being 12.1 mm. (65.3 per cent) and 8.2 (30.7 per cent) in the case of "large" clams.

6. The rates of growth during the "summer" and "fall" seasons (1932) at the Bideford River are approximately the same in contrast to the Clam Cove area where during 1931, "summer" growth clearly predominated. During the "summer" period, the extent of growth was nearly double that occurring at Clam Cove, N. B., where the average daily water temperature was about 9° C. less than in the Gulf of St. Lawrence area.

7. The annual absolute increment of growth in the Bideford River region was found to be 19.9 mm. (87.2 per cent) for specimens having an initial length of 22.8 mm. and in the case of larger specimens (initial length 30.4 mm.) the absolute increment obtained was 18.6 mm. (61.1 per cent). In 1933, clams which set during that year attained a length of about 11 mm. by the end of the growing season.

8. Evidence is presented to support the contention that in warmer waters the rate of growth is more rapid, the set heavier and the maximum size attained, smaller than in cold regions.

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VARIATIONS IN GROWTH INDICES OF *MYA ARENARIA* L. ON THE ATLANTIC COAST OF NORTH AMERICA¹

CURTIS L. NEWCOMBE

University of Maryland

AND

HERMAN KESSLER

Hahnemann Medical College of Philadelphia

INTRODUCTION

The object of this study has been to determine certain growth dimensional ratios of *Mya arenaria* and to ascertain the extent of the variations in linear and weight indices characterizing specimens from widely separated regions. The presentation is limited to actual data on geographical growth variations without attempting to give an adequate explanation for these differences. It is believed, however, that local environments are mainly responsible for the variations observed.

The term environment is employed in the sense of the "geographical landscape" of Berg ('26, p. 264), *i.e.* "a region in which the characters of the relief, climate, vegetation, and soils are united in one harmonious whole, which is typical of a certain zone of the earth, recurring throughout its entire area." It is recognized as a *complex* of the interaction of different factors and thus interpreted broadly rather than in the limited sense discussed by Allen ('29, p. 226). Following Vladikov ('34, p. 100) reference to "environmental influences" signifies the influence of the environmental complex whereas in the limited sense, we have used "environmental factors."

Present knowledge does not permit a thorough understanding of the most significant variables in the environments studied. The findings of Belding ('16) and Newcombe ('35b) justify the recognition of temperature, soil and salinity as primary factors affecting the character of growth in this pelecypod. These environmental factors are briefly described for the four regions considered—namely, Bay of Fundy, Gulf of Maine, Gulf of St. Lawrence, and Chesapeake Bay—and their seeming effect on the several growth indices discussed. No attempt has been made to review the numerous recent publications dealing with differential growth ratios and the effect on these of environment.

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¹ Contribution from the Zoological Laboratory of the University of Maryland and the Chesapeake Biological Laboratory.

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METHODS

A. Methods of Measurement

The linear dimensions—length, width and thickness—were measured with a sliding vernier caliper reading to 0.1 mm. Length implies the greatest anterior-posterior dimension; width, the maximum dorso-ventral dimension; and thickness refers to the greatest distance between the two valves of the tightly closed animal placed in a lateral position.

Specimens collected for the purpose of weighing were kept in fresh, circulating salt water immediately after removal from the beach. In this way, individual variation that might result from the presence of sand particles within the valves was reduced. All specimens were dried in air to a constant weight in an oven at about 70° C.

Length has been employed as the basic index of size, and the other dimensions described in terms of this index. As is clearly pointed out by Weymouth ('23, p. 21), from a purely mathematical viewpoint, length is just as good but no better a measure of size than weight. In practice it is far more serviceable and hence more generally accepted.

B. Methods of Biometrical Analysis

Regional collections were divided into groups and the mathematical constants of each derived. The nature of the material available has not permitted an ideal system of grouping. The reliability of the several mean dimensions obtained is expressed in tabular form. The range of possible error in measurement varies with size but it has been determined experimentally that this source of variation does not significantly influence the means of the several groups.

Constants for the equations—(1) $W = e + fL$, (2) $T = i + kL$, (3) $Wt = cL^k$ —expressing the relation of width (W), thickness (T) and weight (Wt) to length have been obtained by the method of Lipka ('18). In the case of one group the method of least squares was used also and no significant difference obtained hence the application of the shorter method.

REGIONAL DESCRIPTIONS

The complexity of the factors operating in the littoral environment and the limited extent of our knowledge of these factors render a regional com-

parison somewhat difficult. The probable importance of temperature, soil and salinity producing variations in growth dimensional ratios is recognized. Therefore, in the descriptive comparison of the four regions studied, these particular factors are stressed.

A. Bay of Fundy Region

A high tidal amplitude of over 25 feet constitutes the dominant characteristic of the littoral zone of the Bay of Fundy Region. It determines the incidence of practically all other factors. The resultant mixing of surface with subsurface waters modifies the thermal conditions to which *Mya* is exposed. Table I shows the monthly trend of temperatures throughout the year taken

TABLE I. *Temperatures taken at the Atlantic Biological Station Wharf, St. Andrews, New Brunswick and in the Bideford River, Prince Edward Island*
Mean Monthly Temperatures *

Time in months	St. Andrews				Bideford River 1932 Water ° C.
	1931 Water ° C.	Air ° C.	1932 Water ° C.	Air ° C.	
January	2.96	-6.42	3.01	-1.98	
February	1.71	-5.52	0.71	-7.97	
March	1.68	0.72	0.72	-2.91	
April	3.72	5.34	3.29	3.34	
May	6.63	10.26	6.29	9.57	(May 13-31) 14.1
June	9.63	14.85	9.03	14.46	16.9
July	12.37	18.22	11.37	16.69	20.4
August	13.23	18.18	13.11	17.58	21.8
September	12.23	13.43	12.91	16.04	17.2
October	10.93	9.52	11.35	9.12	11.6
November	8.58	5.65			3.4
December	4.71	-3.37			

* Monthly mean water temperatures represent the mean of daily mean temperatures based on the average of two surface readings taken about 8 A.M. and 5 P.M. Mean air temperatures represent the mean of daily mean temperatures obtained by calculating the mean of the maximum and minimum daily temperatures.

at the Atlantic Biological Station Wharf, St. Andrews, New Brunswick.—Lat. 45° 2' (area from which collection was made). Available information indicates that the range of temperature for growth of *Mya arenaria* in this latitude is from about 6° C. to 13° 5 C. and that little growth occurs before May 1st and after September first (Newcombe, '35a). The lowest water temperatures (below 2° C.) prevail during February and March whereas the highest mean monthly temperatures, ranging over 12° C., obtain during July, August, and September.

The soil of the typical *Mya* beaches of this region consists of a mixture of sand and mud in varying proportions depending on the intertidal level. (In this region, *Mya* is restricted, in the main, to the zone above the mean low water level.) Generally, mud is plentiful, the mixture forming a fairly firm soil surface.

In the more exposed areas the salinity of the water is subject to very slight variations ranging at the mouth of the Bay from about 28 to 33 per mille (compare Newcombe, '30).

B. Gulf of Maine

The collection representing the Gulf of Maine region (southern part) was taken in Plymouth Harbor, Mass.—Lat. $41^{\circ} 57'$. Here, the tidal amplitude is approximately seven feet above chart datum. Temperatures during the growing season are significantly higher than in the St. Andrews area (Bay of Fundy). Unfortunately comparable records are not available. In the shallow waters over the *Mya* beaches, the temperature rises more rapidly in spring and maintains a higher mean throughout the growing season than in the Bay of Fundy. An appreciation of the downward trend of temperature in the direction of the Bay of Fundy is given by Bigelow ('27, figs. 29, 31). Available data would indicate a mean temperature of the beach waters during July and August of at least 17° C.

The Plymouth Harbor collection was taken from a beach composed of dark soil representing a mixture of mud and sand, the former definitely predominating. In comparison with the soil conditions in the area of collection of the Bay of Fundy, there seems to be little difference except possibly less mud is present in the latter area.

The mean salinity of the Gulf of Maine falls close to 32.5 per mille (Bigelow, '27, p. 702). In inshore areas, due to the influx of land waters, records as low as 27 per mille obtain.

C. Gulf of St. Lawrence

The collection from this region was made at a point about two miles above the mouth of the Bideford River, an inlet tributary to Malpeque Bay, Prince Edward Island, located on the south shore of the Gulf—Lat. $46^{\circ} 30'$. The beach possesses an intertidal zone that forms a narrow belt along the shore approximately ten meters in width. The average rise and fall of tide is about 3 feet.

Temperatures during the growing season are significantly higher than those at Plymouth Harbor—Gulf of Maine. This statement does not apply to the deeper waters of the Gulf where temperatures are about the same (Bigelow, '27, p. 701). Unfortunately comparable monthly means are not available. A comparison of the monthly trend of temperatures with that of the Bay of Fundy region is presented in table I. In the latter region during the greater part of the growing season, the mean water temperature is about 9° C. less (compare Newcombe, '36).

Sand is the predominant soil type of the Bideford River beach although some mud is present in the area of collection, its proportion being very small in comparison with that characterizing the aforementioned regions.

The salinity of the Bideford River waters has been found to be quite similar to that of the Bay of Fundy area (Needler, '31).

D. Chesapeake Bay

The *Mya* collection of this region was taken near the Chesapeake Biological Laboratory located at the mouth of the Patuxent River—Lat. $38^{\circ} 19'$. This region is characterized by a small tidal amplitude not exceeding 3 feet and by a very narrow intertidal zone (vertical distance from mean low water level to mean high water level about 10 meters). Although available temperature data are not complete enough to permit a direct comparison with those of the Gulf of St. Lawrence region (table I), they do show, definitely, a significantly higher trend during the active season. During the period from June 26 to August 4, 1935, the mean of daily mean temperatures² taken at the pier of the Chesapeake Biological Laboratory was found to be 26.1°C . Fairly comparable means for the Gulf of St. Lawrence and Bay of Fundy regions are 20°C . and 11°C ., respectively (Newcombe, '35a). During March, temperatures as high as 11°C . frequently obtain and as late as October the surface temperature is around 20°C .

Edaphic conditions of the area from which the Chesapeake collection was made are quite similar to those in the Gulf of St. Lawrence region. The soil is dark and consists of a mixture of sand and mud in which the former clearly predominates. Both these areas differ from the Bay of Fundy in that the soil is not nearly as compact.

In the regions described above, variations in salinity have not been marked. In this area, the salinity is relatively low, remaining between 11 and 13 per mille the greater part of the year, rarely if ever reaching 15 per mille in winter (compare Cowles, '30, pp. 284–288). The significance of this pronounced decrease in comparison with the other three regions is discussed in a later part of this paper.

RESULTS

A. Linear Dimensions

Length-width and length-thickness growth dimensional ratios of *Mya arenaria* have been evaluated for the four regions under consideration (Figs. 1, 2). In table II the "a" and "b" values obtained for the length-width and length-thickness ratios are presented. Calculated values for width and thickness corresponding to the mean lengths of the several groups considered have been obtained (table III). These values may be readily compared with the actual means. The mathematical constants of the frequency distributions of the widths and thicknesses for the four regions are given in table IV.

² The mean water temperature, 26.1°C . represents the mean of daily mean temperatures based on the average of two surface readings taken about 8 A.M. and 5 P.M.

TABLE II. *Constants of the functions W (or T) = $a + bL$ and $Wt = cL^k$ in which W = width, T = thickness, Wt = weight and L = length*

		Bay of Fundy	Gulf of Maine	Gulf of St. Lawrence	Chesapeake Bay
Length	<i>b.</i>	0.595	0.545	0.558	0.604
Width	<i>a.</i>	1.135	2.042	1.531	-0.644
Length	<i>b.</i>	0.376	0.345	0.351	0.404
Thickness	<i>a.</i>	0.161	0.657	0.237	-1.589
Length	<i>k.</i>	3.410	3.140	3.127	3.481
Shell weight	<i>c.</i>	0.00001223	0.00002177	0.00001887	0.000004139
Length	<i>k.</i>	3.119			3.300
Body weight	<i>c.</i>	0.00000443			0.000002607

TABLE III. *Growth indices in millimeters of *Mya arenaria**

Group No.		Length Range	Mean Length	Width Range	Mean Width Act.	Mean Width Calc.	Thickness Range	Mean Thickness	
								Act.	Calc.
Bay of Fundy									
1	10	14.5- 17.7	15.94	9.2-11.6	10.38	10.61	5.2- 6.4	5.66	6.15
2	15	20.0- 23.1	21.05	12.5-17.8	13.88	13.65	6.8- 9.1	7.71	8.08
3	15	25.6- 39.5	33.14	16.1-24.9	21.07	20.84	9.4-15.5	12.31	12.63
4	19	40.1- 49.3	45.46	24.6-34.3	28.18	28.16	14.9-21.9	17.51	17.27
5	15	50.4- 59.2	54.35	29.8-37.6	33.03	33.47	19.1-22.4	20.32	20.61
6	52	60.0- 69.5	65.02	34.8-45.3	40.39	39.82	21.5-30.9	25.00	24.62
7	31	70.3- 81.6	74.20	40.1-50.6	44.48	45.28	24.6-31.2	27.40	28.08
Gulf of Maine									
1	15	14.1- 20.0	16.80	9.0-12.6	10.80	11.19	5.2- 8.0	6.24	6.45
2	12	24.5- 34.5	29.50	15.0-21.1	18.60	18.11	8.9-13.1	10.80	10.82
3	12	37.8- 50.0	43.90	22.6-33.1	26.30	25.95	12.8-21.5	15.90	15.78
4	15	62.5- 71.4	67.11	37.1-43.6	40.30	38.59	21.4-25.6	23.70	23.78
5	15	73.6- 81.4	77.99	40.6-49.1	45.60	44.52	23.6-33.6	27.52	27.56
6	15	94.6-107.8	101.02	55.3-63.1	59.40	57.05	34.6-40.2	37.60	35.53
Gulf of St. Lawrence									
1	15	13.4- 17.3	15.38	8.2-10.3	9.32	10.10	4.6- 6.4	5.53	5.63
2	15	26.5- 32.2	29.06	15.9-20.2	17.93	17.75	9.5-11.1	10.31	10.48
3	15	36.0- 42.8	39.19	22.9-26.6	24.43	23.38	12.3-15.5	14.14	14.02
4	15	42.3- 47.7	45.38	24.8-29.3	27.26	26.83	13.2-17.7	16.23	16.16
5	10	51.4- 56.7	53.50	29.2-33.1	31.20	31.36	17.3-19.5	18.29	19.01
6	10	60.1- 64.1	62.10	24.6-41.4	35.78	36.15	20.3-22.3	21.09	22.03
7	10	74.4- 80.2	77.83	44.4-48.4	46.23	44.92	26.3-30.3	28.82	27.55
8	10	82.2- 99.8	89.69	43.5-61.7	51.42	51.53	29.9-37.2	32.26	31.70
Chesapeake Bay									
1	43	20.3- 29.6	25.98	12.4-17.4	15.31	15.04	8.1-11.1	9.29	8.89
2	73	30.1- 39.9	34.65	16.1-23.8	19.55	20.28	10.1-15.0	12.02	12.39
3	20	40.0- 49.5	43.38	25.5-30.0	25.15	25.55	12.7-20.4	15.74	15.94
4	15	50.0- 56.9	53.72	28.5-35.5	32.06	31.80	18.4-22.6	20.28	20.01
5	10	60.7- 64.2	62.89	34.0-49.2	38.61	37.34	21.7-27.4	24.30	23.82
6	10	70.0- 82.2	75.96	40.8-50.9	46.05	45.23	25.0-33.6	29.37	29.10

B. Weight Indices of Growth

Analysis of the length-width (shell and dry body weights) data shows that we are justified in saying that growth in weight of *Mya arenaria* may

TABLE IV. *Constants of frequency distributions of Lengths, Widths, and Thicknesses in millimeters of Mya arenaria*

Group No.		Mean Length	Standard Deviation	Mean Width	Standard Deviation	Mean Thickness	Standard Deviation
Bay of Fundy							
1	10	15.9±0.2	0.82±0.1	10.38±0.05	0.20±0.03	5.66±0.08	0.36±0.06
2	15	21.1±0.2	0.9 ±0.1	13.9 ±0.3	1.4 ±0.2	7.7 ±0.1	0.69±0.09
3	15	33.1±1.5	8.1 ±1.0	21.1 ±0.6	3.1 ±0.4	12.3 ±0.8	4.4 ±0.6
4	19	45.5±0.3	1.8 ±0.2	28.2 ±0.4	2.2 ±0.3	17.5 ±0.2	1.5 ±0.2
5	15	54.4±0.5	2.8 ±0.4	33.0 ±0.4	2.2 ±0.3	20.3 ±0.2	1.1 ±0.1
6	52	65.0±0.3	3.5 ±0.2	40.4 ±0.4	4.4 ±0.3	25.0 ±0.4	4.7 ±0.3
7	31	74.2±0.4	3.2 ±0.3	44.5 ±0.3	2.3 ±0.2	27.4 ±0.7	5.7 ±0.5
Gulf of Maine							
1	15	16.8±0.4	2.4 ±0.3	10.8 ±0.3	1.7 ±0.2	6.2 ±0.2	0.8 ±0.1
2	12	29.5±0.6	3.2 ±0.5	18.6 ±0.5	2.3 ±0.3	10.8 ±0.4	1.9 ±0.3
3	12	43.9±0.8	4.3 ±0.6	26.3 ±0.7	3.4 ±0.5	15.9 ±0.7	3.3 ±0.5
4	15	67.1±0.5	2.7 ±0.3	40.3 ±0.4	2.1 ±0.3	23.7 ±0.3	1.6 ±0.2
5	15	77.9±0.3	2.1 ±0.3	45.6 ±0.6	3.1 ±0.4	27.5 ±0.4	2.3 ±0.3
6	15	101.0±0.2	1.1 ±0.1	59.7 ±0.2	1.3 ±0.2	37.6 ±0.3	1.9 ±0.2
Gulf of St. Lawrence							
1	15	15.4±1.1	5.9 ±0.8	9.3 ±0.2	1.2 ±0.2	5.5 ±0.2	0.8 ±0.1
2	15	29.1±0.6	3.1 ±0.4	17.9 ±0.06	0.4 ±0.05	10.3 ±0.3	1.5 ±0.2
3	15	39.2±0.8	4.3 ±0.6	24.4 ±0.4	2.4 ±0.3	14.1 ±0.5	2.5 ±0.3
4	15	45.4±0.7	3.6 ±0.5	27.3 ±0.7	4.1 ±0.5	16.2 ±0.2	0.8 ±0.1
5	10	53.5±0.4	1.9 ±0.3	31.2 ±0.9	4.1 ±0.7	18.3 ±0.6	2.7 ±0.4
6	10	62.1±1.3	6.0 ±1.0	35.8 ±0.3	1.2 ±0.2	21.1 ±0.2	1.0 ±0.2
7	10	77.8±1.0	4.6 ±0.7	46.2 ±1.0	4.4 ±0.7	28.8 ±0.4	1.9 ±0.3
8	10	89.7±0.4	1.8 ±0.3	51.4 ±0.2	1.0 ±0.2	32.3 ±0.2	0.7 ±0.1
Chesapeake Bay							
1	43	26.0±0.3	2.4 ±0.2	15.3 ±0.1	1.10±0.09	9.29±0.08	0.83±0.06
2	73	34.7±0.2	2.7 ±0.2	19.6 ±0.1	1.8 ±0.1	12.02±0.06	0.80±0.05
3	20	43.4±0.2	1.5 ±0.2	25.2 ±0.6	3.6 ±0.4	15.7 ±0.3	2.0 ±0.2
4	15	53.7±0.4	2.0 ±0.3	32.1 ±0.4	2.1 ±0.3	20.3 ±0.3	1.5 ±0.2
5	10	62.9±0.5	2.4 ±0.4	38.6 ±0.9	3.8 ±0.6	24.3 ±0.4	1.7 ±0.3
6	10	76.0±0.8	3.6 ±0.6	46.1 ±0.8	3.4 ±0.5	29.4 ±0.7	3.0 ±0.5

be expressed by the equation of a constant differential growth-ratio, namely, $Wt = cL^k$. Values of the constants c and k for shell weights have been determined for the four regions studied whereas corresponding values for body weights are known only for the Bay of Fundy and Chesapeake Bay (table II). On a basis of these constants, calculated weights corresponding to the means of the several groups of each region have been obtained. In table V these calculated values are compared with the corresponding actual mean weights (figs. 3, 4). Mathematical constants for the frequency distributions of shell weights and dry weights of body parts are presented in tables VI and VII.

DISCUSSION

With respect to linear indices of growth of *Mya arenaria* from the four regions considered, it is shown in table II that a close parallelism exists with respect to regional variations in the two growth dimensional ratios consid-

TABLE V. *Growth Indices in millimeters and grams of Mya arenaria*

Group	No.	Mean Length	Shell Weight		No.	Mean Length	Mean Body Weight	
			Act.	Calc.			Act.	Calc.
Bay of Fundy								
1	19	15.86	0.159	0.153			0.024	0.025
2	32	26.30	0.802	0.850			0.111	0.119
3	19	34.76	2.105	2.200			0.296	0.284
4	19	47.24	7.225	6.263			0.987	0.740
5	30	54.58	11.385	10.350			1.425	1.160
6	29	65.08	19.365	18.670			2.082	2.009
7	13	73.47	25.446	28.240			2.261	2.932
8	8	84.44	35.652	45.390			3.262	4.526
Gulf of Maine								
1	14	16.64	0.141	0.149				
2	18	25.67	0.724	0.582				
3	6	33.71	1.118	1.365				
4	13	44.50	4.413	3.264				
5	11	66.49	12.198	11.520				
6	15	76.98	18.605	18.240				
7	15	108.11	49.947	52.980				
Gulf of St. Lawrence								
1	15	15.38	0.116	0.097				
2	10	28.26	0.639	0.652				
3	15	35.75	1.336	1.359				
4	20	44.38	2.512	2.674				
5	10	53.50	4.264	4.797				
6	10	62.10	6.881	7.646				
7	9	77.57	18.131	15.330				
8	11	88.83	27.537	23.420				
Chesapeake Bay								
1	39	25.98	0.381	0.348	32	25.36	0.098	0.112
2	47	35.94	0.876	0.928	35	34.68	0.294	0.315
3	9	46.41	2.966	2.625	9	46.41	0.989	0.824
4	15	53.72	4.719	4.378	15	53.70	1.586	1.333
5	10	62.89	7.213	7.352	10	62.39	2.507	2.187
6	10	75.96	13.949	14.670	4	76.90	3.817	4.360

ered, *i.e.*, the order of increase of "b" values for length-width relations in the four regions is the same as that for the length-thickness ratio.

Mathematically the "b" value represents the rate of increase of width or thickness relative to the basic index length. The greatest variation in the "b" values for length-width ratios observed, namely 11 per cent, is that between the Chesapeake Bay and the Gulf of Maine regions. Corresponding to this, there is an 18 per cent variation in the length-thickness "b" value for the same two regions. A similar relation holds for the Bay of Fundy and the Chesapeake Bay. No significant variation in "b" values obtains for the Gulf of Maine and the Gulf of St. Lawrence areas.

TABLE VI. *Constants of frequency distributions of shell weights in grams of Mya arenaria*

Group No.	Length Interval	Mean Length in mm.	Shell Weight Range	Mean Shell Weight	Standard Deviation	
Bay of Fundy						
1	19	10.0- 19.9	15.86	0.071- 0.332	0.159±0.012	0.077±0.008
2	32	20.0- 29.9	26.30	0.410- 1.332	0.802±0.031	0.26 ±0.022
3	18	30.0- 39.9	34.76	1.314- 2.892	2.105±0.12	0.75 ±0.087
4	19	40.0- 49.9	47.24	3.900-10.645	7.225±0.27	1.70 ±0.19
5	30	50.0- 59.9	54.58	7.890-17.742	11.385±0.35	2.80 ±0.25
6	29	60.0- 69.9	65.08	14.230-24.760	19.365±0.36	2.80 ±0.25
7	13	70.0- 79.9	73.47	18.047-31.690	25.446±0.68	3.50 ±0.48
8	8	80.0- 89.9	84.44	30.627-44.790	35.652±1.09	4.30 ±0.78
Gulf of Maine						
1	14	10.0- 19.9	16.64	0.076- 0.273	0.141±0.009	0.050±0.01
2	8	20.0- 29.9	25.67	0.270- 1.440	0.724±0.08	0.31 ±0.06
3	6	30.0- 39.9	33.71	1.133- 1.947	1.118±0.28	0.94 ±0.20
4	13	40.0- 49.9	44.50	1.765-10.520	4.413±0.51	2.6 ±0.36
5	11	60.0- 69.9	66.49	10.851-14.992	12.198±0.88	4.1 ±0.62
6	15	70.0- 79.9	76.98	12.282-21.736	18.605±0.63	3.5 ±0.45
7	15	100.0-115.9	108.11	42.063-57.387	49.947±0.69	3.8 ±0.48
Gulf of St. Lawrence						
1	15	10.0- 19.9	19.38	0.087- 0.155	0.116±0.004	0.022±0.003
2	10	20.0- 29.9	28.26	0.454- 0.870	0.639±0.03	0.13 ±0.02
3	15	30.0- 39.9	35.75	0.670- 1.930	1.336±0.08	0.47 ±0.06
4	20	40.0- 49.9	44.38	1.065- 3.350	2.512±0.09	0.56 ±0.06
5	10	50.0- 59.9	53.50	3.698- 4.878	4.264±0.08	0.37 ±0.06
6	10	60.0- 69.9	62.10	5.245- 8.306	6.881±0.22	0.96 ±0.15
7	9	70.0- 79.9	77.57	15.533-19.018	18.131±0.17	0.71 ±0.12
8	11	80.0- 89.9	88.83	20.893-50.017	27.537±1.60	7.60 ±1.20
Chesapeake Bay						
1	39	20.0- 29.9	25.98	0.149- 0.526	0.381±0.01	0.062±0.005
2	47	30.0- 39.9	35.94	0.501- 1.593	0.876±0.03	0.33 ±0.02
3	9	40.0- 49.9	46.41	1.830- 4.460	2.966±0.18	0.77 ±0.13
4	15	50.0- 59.9	53.72	3.400- 5.855	4.719±0.12	0.67 ±0.09
5	10	60.0- 69.9	62.89	5.930- 9.350	7.213±0.41	1.80 ±0.29
6	10	70.0- 79.9	75.96	10.470-18.750	13.949±1.50	6.50 ±1.03

TABLE VII. *Constants of frequency distributions of weights of body parts in grams of Mya arenaria*

Group	No.	Mean Length in mm.	Range of Body Weight	Mean Body Weight	Standard Deviation
Bay of Fundy					
1	19	15.86	0.009-0.048	0.024±0.002	0.010±0.001
2	32	26.30	0.062-0.246	0.111±0.008	0.066±0.006
3	18	34.76	0.115-0.786	0.296±0.03	0.160±0.02
4	19	47.24	0.428-1.620	0.987±0.06	0.380±0.04
5	30	54.58	0.847-2.756	1.425±0.11	0.850±0.08
6	29	65.08	0.820-3.459	2.082±0.07	0.510±0.05
7	13	73.47	1.551-3.622	2.261±0.14	0.720±0.10
8	8	84.44	2.983-4.002	3.262±0.11	0.43 ±0.08
Chesapeake Bay					
1	32	25.36	0.048-0.163	0.098±0.004	0.030±0.003
2	35	34.68	0.160-0.499	0.294±0.01	0.061±0.005
3	9	46.41	0.660-1.395	0.989±0.12	0.520±0.090
4	15	53.70	0.980-2.930	1.586±0.11	0.600±0.080
5	10	62.39	1.650-3.210	2.507±0.13	0.590±0.090
6	4	76.90	3.050-4.890	3.817±0.28	0.710±0.200

The comparison of the widths obtained for the different regions shown in figure 1 indicates that within the length range studied a maximum variation exists between the Bay of Fundy and the Gulf of Maine specimens, in

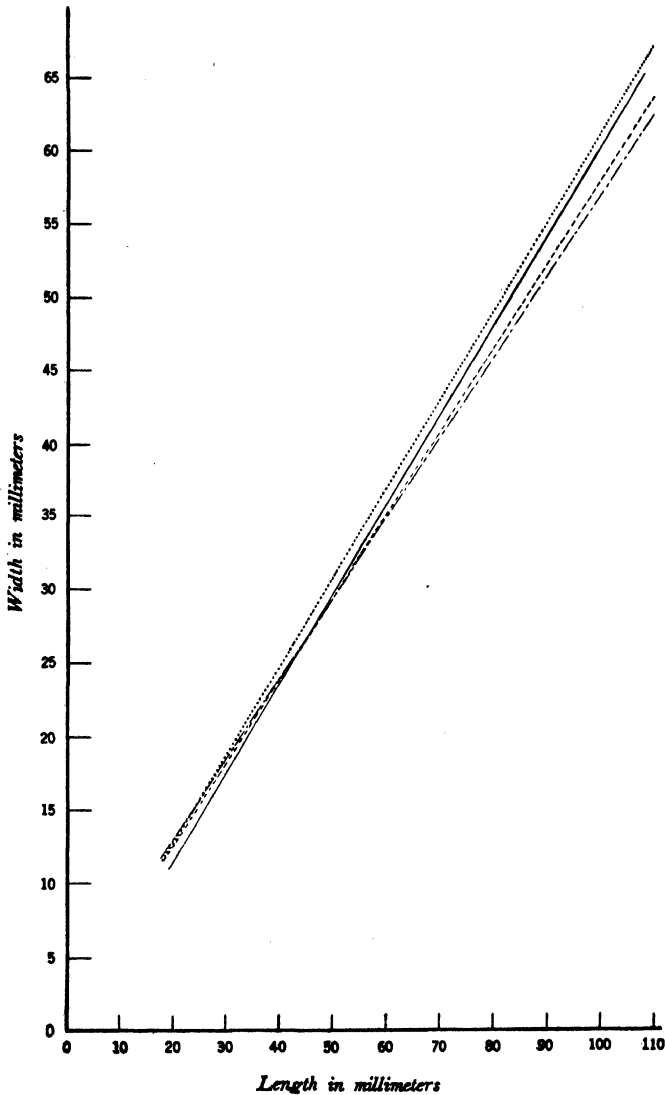


FIG. 1. Showing length-width relations of *Mya arenaria* from four regions of the Atlantic Coast. Dotted line = Bay of Fundy, $W = 1.135 + 0.595 L$; Broken line = Gulf of Maine, $W = 2.042 + 0.545 L$; Dashed line = Gulf of St. Lawrence, $W = 1.531 + 0.558 L$; Continuous line = Chesapeake Bay, $W = -0.644 + 0.604 L$.

no case exceeding 6 per cent. In general, the percentage variation between any two of the regions is less than 6 per cent.

In the case of the thickness dimension, a maximum variation obtains between the Gulf of Maine and the Chesapeake Bay, namely 10 per cent.

Throughout the greatest part of the length range employed, regional variations are below 10 per cent (fig. 2).

Comparing the " k " values which represent the ratios of the relative growth rates of shell and dry body weights as compared with lengths, for the

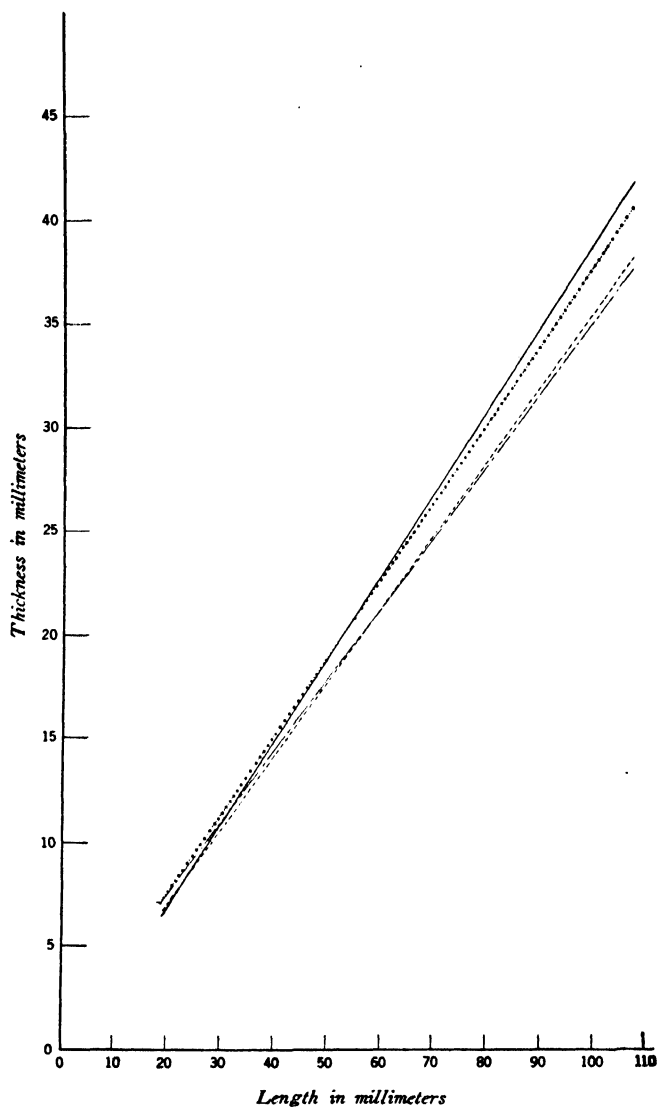


FIG. 2. Showing length-thickness relations of *Mya arenaria* from four regions of the Atlantic Coast. Dotted line = Bay of Fundy, $T = 0.161 + 0.376 L$; Broken line = Gulf of Maine, $T = 0.657 + 0.345 L$; Dashed line = Gulf of St. Lawrence, $T = 0.237 + 0.351 L$; Continuous line = Chesapeake Bay, $T = -1.589 + 0.404 L$.

different regions, it is shown that the maximum variation (shell weight) of 11 per cent exists between the Bay of Fundy and the Chesapeake Bay regions. The value for the dry body weights of the Chesapeake Bay region is approximately 6 per cent greater than that for the Bay of Fundy.

A striking variation is found in the actual shell and dry body weights corresponding to a given length. A comparison of these variations with the mean temperatures of the regions indicates in the main an inverse relationship with respect to shell weight and temperature, but a direct variation of body weight and temperature. A maximum difference exists between the Bay of Fundy and the Chesapeake Bay, the shell weight of the former being more than twice as heavy for a given length (fig. 3). Body weights for

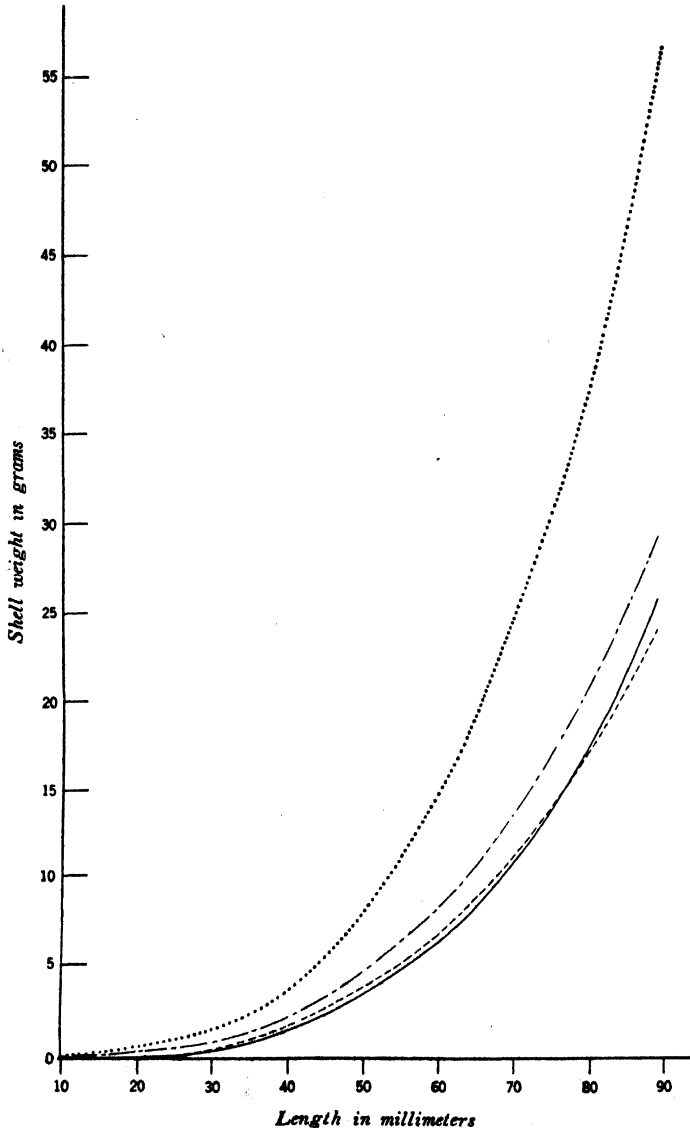


FIG. 3. Showing length-shell weight relations of *Mya arenaria* from four regions of the Atlantic Coast. Dotted line = Bay of Fundy, Wt. = .00001223 $L^{3.410}$; Broken line = Gulf of Maine, Wt. = .00002177 $L^{3.140}$; Dashed line = Gulf of St. Lawrence, Wt. = .00001887 $L^{3.127}$; Continuous line = Chesapeake Bay, Wt. = .000004139 $L^{3.481}$.

the two regions, although quite similar in young specimens, tend to differ significantly with increase of shell length (fig. 4).

In light of available data it would seem safe to conclude that variations in the environmental influences of the four widely separated regions are not noticeably reflected in the linear growth dimensional ratios with the possible

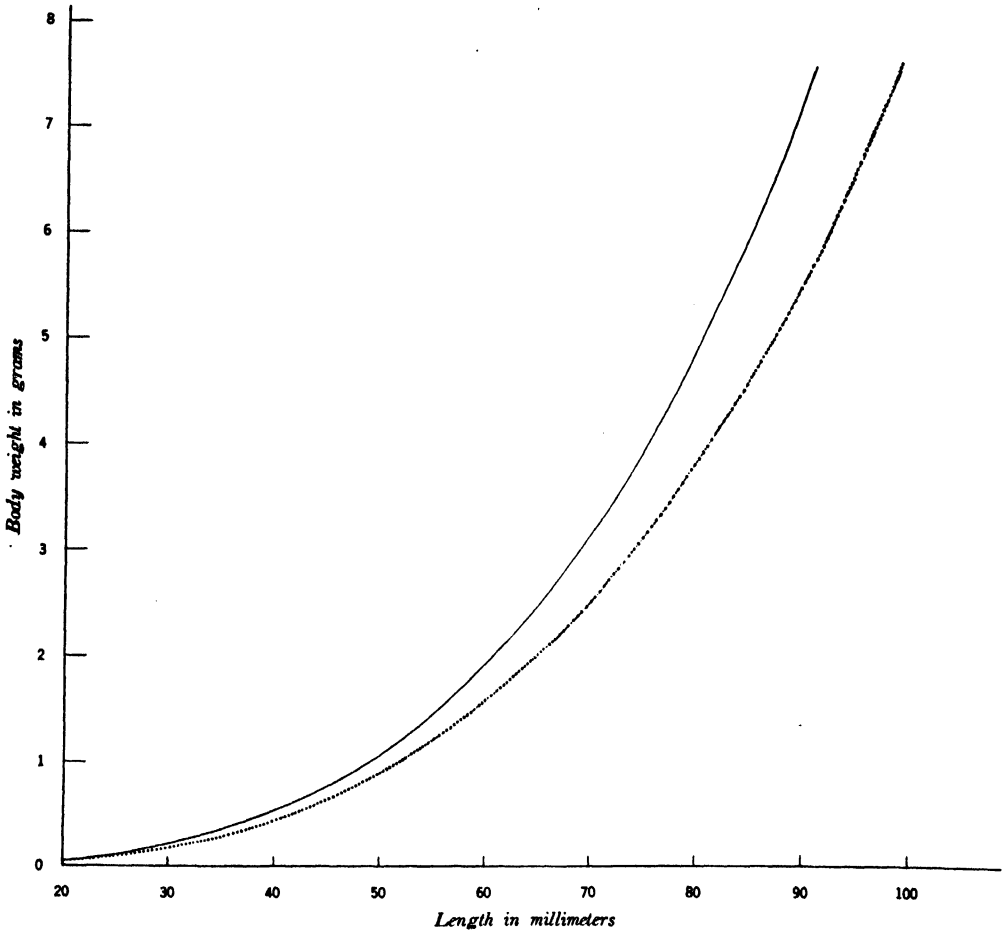


FIG. 4. Showing length-body weight relations of *Mya arenaria* from two regions of the Atlantic Coast. Dotted line = Bay of Fundy, Wt. = .00000443 $L^{3.119}$; Continuous line = Chesapeake Bay, Wt. = .000002607 $L^{3.300}$.

exception of the Gulf of Maine and Chesapeake Bay regions. Certain local variations in linear ratios have been observed in individual specimens within a single region (compare Belding, '16). It is believed, therefore, that if sufficient data were available to give average values for each region thereby ruling out differences due to local factors, the regional variations pointed out above and based on single collections only, might be smoothed out considerably. No apparent correspondence seems to exist between the regional varia-

tions in the environmental factors considered and the variations found in linear growth dimensional ratios.

In the case of the length-weight ratios a different relation seems to hold. Environmental influences operating in the respective areas are, as pointed out above, noticeably different. A fairly close correspondence is evident between weight of shell and the temperature factor, an inverse ratio seeming to exist. It is true that pronounced salinity variations occur between certain of the above-mentioned regions, *e.g.*, Bay of Fundy and Chesapeake Bay (approximately 32 and 11 per mille). However a marked difference is observed in shell weights between the Bay of Fundy and the Gulf of Maine regions, which possess similar salinities (fig. 3). Consequently, in this case at least, some other factor or set of factors of the environmental complex must operate to produce the weight variation. Again, soil differences, as previously shown, are marked between the Bay of Fundy and the Gulf of St. Lawrence and accompany a variation in shell weight. Fairly comparable edaphic conditions exist in the Bay of Fundy and the Gulf of Maine where distinct shell weight differences occur. For this reason, it seems more plausible to regard temperature as the most significant environmental variable. The apparent correspondence revealed in figure 3 is at best only suggestive. The most significant feature of the results lies in the extent of the variations themselves. These differences are fundamental in a consideration of latitude and rates of growth (compare Weymouth, McMillan and Rich, '31, pl. 246).

For specimens above 18 mm. in length, a direct relation has been found to exist between dry body weights and temperature for the two aforementioned regions (fig. 4). *Mya arenaria* of the Chesapeake Bay are known to live at a greater depth in the soil and to possess conspicuously longer siphons than Bay of Fundy specimens of similar length. The implication is, of course, only suggestive.

SUMMARY

1. Linear and weight indices of size have been studied in *Mya arenaria* from four widely separated regions of the Atlantic Coast.

2. The various constants of the linear and weight growth dimensional ratios characterizing the several regions have been compared with the most significant variables of the different environments.

3. The maximum variations revealed in the "b" values for the linear dimensions of *Mya* from the different regions are appreciable whereas differences in the actual widths and thicknesses of corresponding lengths are not considered significant.

4. A striking variation has been found in the shell weights and dry body weights of specimens from the four regions. Shell weights of the Bay of Fundy specimens are approximately twice as heavy as those of similar lengths in the Chesapeake Bay. Shell weights for the Gulf of Maine and Gulf of St. Lawrence regions fall within these two extremes and in the order

named. In contrast to the above relation, body weights for specimens over 18 mm. in length of the Chesapeake Bay are significantly greater than those of the Bay of Fundy.

5. No significant correspondence exists between linear growth dimensional ratios and environmental influences whereas shell weights seem to correspond very closely with the temperature factor, an inverse relation resulting. In the case of dry body weights an opposite trend has been found.

6. The fairly constant nature of the linear growth dimensional ratios and the significant variability of the weight indices in the different latitudes considered indicates that care must be exercised in the selection of a standard size index upon which to base experimental results.

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IS THE SYNUSIA AN ASSOCIATION?

H. A. GLEASON

The New York Botanical Garden

The concept of the association has been before botanists for a century. Upon it and around it has been developed the science known as geobotany or synecology and over it has been waged many a controversy, without any agreement of widespread acceptance as to its meaning. Numerous definitions have been propounded and just as many have been abandoned. Some synecologists still disagree whether the association is an abstract concept or a concrete entity.

Every one must agree, however, that there are detached areas of vegetation which differ distinctly from the surrounding vegetation. In many of these the vegetation is composed of distinct layers or strata, differing from each other not only in their species, but also in the environment and in the life-form of the individuals. For a century, the unit-group in the study of vegetation has been defined to include all the strata superposed on one area, while the different layers have been construed merely as minor but recognizable members of this unit.

Recently Lippmaa ('31, '33) has advocated the idea that each of these layers or synusiae should be regarded as a unit. Several different units may therefore occupy the same area, each of them a representative of a different association. Opinions differ as to the effect of such a choice of a basic synecological unit. Some apparently believe that the total number of synusiae in any region will be little greater than the number of associations recognized under the orthodox view. Others think that it will lead to the delimitation of innumerable minute associations. Apart from any results of Lippmaa's line of reasoning, there are some underlying features of vegetation which may easily be forgotten and which apparently need repeating at fairly brief intervals.

Let us consider any portion of what is ordinarily known as a *stand*, *individu d'association*, *Bestand*, or *piece of vegetation*, restricting this portion to an area no greater than is covered by a single individual of the largest species present; in the figure, this area is represented by A-B. Besides this single individual, except in one-layered associations, other individuals of different species will be present. While these plants share the same *area*, they do not occupy the same space, except to a very minor degree, and the figure has been constructed to indicate as much. Nevertheless, these plants have definitely an influence on each other. To select perfectly obvious examples, it is clear that the larger plant affects the light and, through its

leaf-fall, the soil-environment of the smaller, while the latter intercepts rain-water and reduces the light for seedlings of the larger one.

The two plants have intersecting spheres of influence; each interferes with the environment of the other.

Widening the extent of such a sphere of influence does not necessarily increase its effect, but merely carries its effect over to other individuals not now to be considered. Intensifying the influence of either plant within its sphere has a direct effect on the life and well-being of the other. It may act either favorably or unfavorably. In the former case it leads to greater vegetative activity of the present generation or to a better opportunity for reproduction. Unfavorably, it may lead to suppression of growth, failure

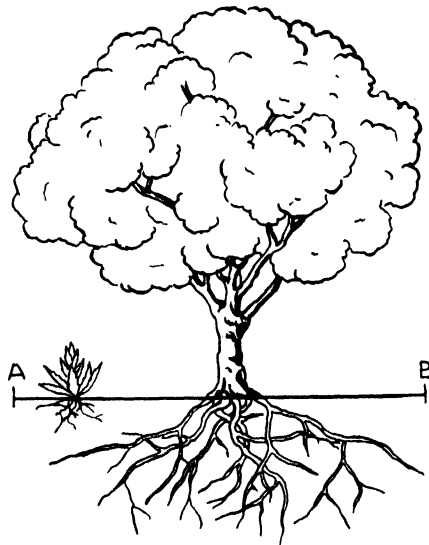


FIG. 1. A simple plant community.

of reproduction, or actual death. By proper methods, the nature of the interference may sometimes be learned. Toumey, ('29) for example, showed that the herbaceous layer under pines developed far better when withdrawal of water by tree roots was prevented.

It is obvious that all plants occupy space and area, but nevertheless many of their functions can be considered without reference to either. In the case in point, we are dealing with a matter of physiological interference, which, although located *in* an area, is not a function *of* the area. Increasing or decreasing the size of the area does not affect either its nature or its intensity.

We can easily satisfy ourselves that a similar interference obtains over areas of considerable extent and that throughout this extent the results of the interference are the same. We must remember, however, that the nature of these results varies with the intensity of the interference. Accordingly the vegetation, which is the result of the interference, varies from time to time

on any one spot and varies from spot to spot at any one time. In spite of all this, the general nature of the interference remains the same, and any one spot may bear, or may have borne, the same vegetation at a different time, while any two spots may or may not bear the same vegetation at any one time.

In the above paragraph, the phrase "same vegetation" indicates vegetation of such similarity, both in kinds of species and number of individuals, that even statistical analysis fails to discover any obvious differences.

If we compare different and separated areas of the same synusia, and now for the first time introduce the concept of area into our speculation, we note at once that the sphere of influence of any individual plant does not extend laterally, except within very restricted distances of space (quantitatively) or except in a very minor degree (qualitatively). The influence of a tree, for example, extends under ground only to the limit of its root system; on the surface only as far as its fallen leaves are carried by the wind in autumn; in control of physical environment only as far as it casts an effective shadow or effectively decreases wind velocity. Qualitatively, as a source of pollen, of seeds, or of fungus-infection, its influence may extend farther, but in these features the degree of its interference is very slight.

As widely in space as a uniform physical environment *and* a uniform physiological interference are maintained, just so widely will the vegetation remain similarly uniform, modified only by the factor of time, which is necessary to the *attainment* of uniformity. Every fluctuation (in time) or variation (in space) of either complex of factors will consequently be reflected in the vegetation. The extent of this reflection is often very slight, but it is nevertheless significant. A late spring may defer blooming of vernal herbs; a severe summer drought may both hasten and limit autumnal blooming. Too much rain in one particular week may decimate the seedlings of one species. Naturally the effect of these minor changes is most pronounced on the rarer species, and I have no doubt that during the next few years will be recorded the complete disappearance of various eastern woodland plants from outlying stations in Kansas, Nebraska, and Iowa, as a result of prolonged drought. Those of us who have been fortunate enough to follow the detailed structure of a single stand of vegetation through a reasonable period of years have certainly seen these changes in time. More conspicuous, but precisely the same in fundamental nature, are the changes in space, exemplifying on two different spots in one year differences in total environment which may easily occur on one spot in two different years.

Almost without exception, every plant community composed of two or more layered synusiae exhibits variations, not only in its physical environment, but also in the degree of physiological interference of the component plants, and these variations exist both in space and time. Accordingly no such community exhibits absolute spatial or temporal uniformity in its vegetation. The recognition of this diversity is the cause which has led to the recent development of such ecological concepts as constance and fidelity. Most de-

tailed analyses of vegetation have extended over space rather than through time; hence these concepts are spatial in nature. If we should instead investigate the composition of vegetation through a period of years, we might easily arrive at a concept of permanence, and this would have the same relation to the broader concept of succession as constance bears to associational extent, while both would relate to matters of associational delimitation.

It is distinctly disclaimed that the general principle advanced above and clearly intended to be a philosophical inquiry into the nature of the vegetational community has any bearing or practical application in the delimitation or recognition of associations in the field. But if this principle is accepted, it leads inevitably to certain other conclusions which may be of practical nature. Before stating them, we shall approach the subject again from a different angle.

Since the first recognition of the plant community, irrespective of the name applied to it, its cause, or its scope, and continuing to the present day, the individual plant community has always been a geographic unit. It occupies space and it has boundaries. Moreover, it exhibits uniformity of structure within the area. Extent, boundary, uniformity: these are the *sine qua non* of every community. Having extent, it must have boundary, and without uniformity both extent and boundary lose all significance. These fundamental features hold under every definition of the community. Differences in definition depend primarily on the nature and degree of uniformity required, and through these extent is increased or decreased and boundary is expanded or contracted. Only one other fundamental feature has been frequently neglected and that is the time relation. There must be boundary in time as well as in space; there must be a beginning as well as an end.

Of these three basic features, uniformity is clearly the most important, since upon it depend both extent and boundary. The nature or degree of uniformity can be described in words, pictured by the camera, analyzed by statistical methods. But what is its cause?

If we re-read the first part of this paper we find the cause. It is two-fold. The first is the existence over a considerable area of an environment which is itself uniform. We can analyze and measure this environment by suitable instruments, but the best estimate of it is found in its results, since it leads, in conjunction with the second cause, to a uniformity of vegetation which is directly related to its own uniformity.

The second is the existence throughout the area of a uniform type of physiological interference. The two together produce over the whole area a complex of minini-area environments, widely differing among themselves, but all uniting to produce a mosaic of environment within which each individual type is repeated numberless times. The result of the environmental mosaic is a vegetational mosaic, composed of numerous types of vegetation each repeated numberless times, but all united into a harmonious and extensive whole.

In a plant community, therefore, the essential nature, the fundamental cause, the real *ens* of its existence, is non-areal, while its manifestation is distinctly areal, characterized by uniformity, extent, and boundary.

Now one can clearly derive from the above statement conclusions similar to those so strongly advocated by Lippmaa. In a maple forest the environmental-complex, as determined both by physical conditions and by physiological interference, is essentially uniform on the bark on the north side of every maple tree. The same kinds of lichens may be found or may be logically expected on the north side of every tree, subject only to local variations or temporary fluctuations in either or both of the two basic causes. Obviously the segregation of such a lichen community is justified from the definition. The herbaceous synusia, also, occupies a stratum in which all the plants have the same environment, subject to the same variation in space and time.

Each component lichen in the former synusia, each herb in the latter, has its own sphere of influence. Now we must note again that these spheres do not extend far laterally. The lichens of one tree do not exert the slightest interference on those of the next tree; the herbs of *this* particular spot do not interfere with those of *that* spot. There is no dynamic connection between different parts of the same synusia, except the possibility of infection with parasites; there is no genetic connection except through pollination and seed production.

On the contrary, the physiological interference of each plant in each synusia (excepting possibly bark-lichens and parasitic fungi) affects to a high degree every plant of the other synusiae which lie within its sphere of influence. There is a direct and important connection between the different synusiae both dynamically and genetically. Every change in the nature or degree of physiological interference is reflected, proportionately to its amount, in the kinds of plants and in the number, vitality, and reproductive capacity of the individuals composing each kind. The same totality of physiological interference, emanating from many individuals, plus the same physical environment, repeated again and again over a wide area, lead to our fundamental feature of uniformity of vegetation. Fluctuations and variations in the same two factors lead to the well known fluctuation and variation in the structure of the vegetation, which is so prominent a feature of every plant community.

To bring together into one ecological unit all those plants with intersecting spheres of influence leads to a unit which not only possesses uniformity, but is also a dynamic and genetic unit. To bring together into one unit only those plants which have exactly the same environment, namely, those which form a single synusia, leads to the divorce of cause and effect.

It has been stated that stands composed of a single synusia afford good evidence for the use of the synusia as a basic concrete unit of vegetation.

If we examine typical examples of such synusia we shall actually find evidence to the contrary.

A swamp occupied by a dense forest of *Thuja occidentalis* may be completely one-layered. If a few trees are blown down by wind or die by disease, so that a very little additional light reaches the forest floor, that spot is at once colonized by numerous mosses. If the break in the forest cover is slightly greater, herbs appear, such as *Moneses uniflora* and *Habenaria clavel-lata*. If a road is opened through such a forest, so that the physiological interference of the trees is not merely modified, but completely eliminated, then, and not until then, plants of a different association appear. Obviously the *Thuja* forest is not one-layered, but three-layered. When only a single layer exists, the other two are merely temporarily suppressed.

Around the margin of certain peat-bog lakes is a definite zone of *Sphagnum*, in which some species of flowering plants grow but constitute a very small proportion of the total bulk of vegetation. Farther from the margin of the water the *Sphagnum* is covered by a taller layer of *Chamaedaphne*. It has been stated that, since the *Sphagnum* zone constitutes a distinct stand of one association and is projected under an equally distinct stand of *Chamaedaphne*, its associational value is not lost, and that the two synusiae of *Chamaedaphne* and *Sphagnum* therefore represent two distinct associations. In answer to this view, let us present the following facts. The zone of *Sphagnum* advances centripetally at a slow rate. The zone of *Chamaedaphne* advances at a rate which may equal or exceed or fall short of the rate of the *Sphagnum*. As a result of uneven rates of advance, instances may be found with a wide zone of *Sphagnum* and others where the *Chamaedaphne* actually reaches the water's edge. Now there can be no doubt that the mobility, potentiality for migration, of *Chamaedaphne* is regularly greater than the slow advance of the *Sphagnum*, and scattered plants of it may often be found far ahead of the bulk of the species. Evidently there is something in the environment of the *Sphagnum* which interferes with the ecesis of *Chamaedaphne*. When this factor is finally sufficiently changed, *Chamaedaphne* appears. Apparently this factor is a function of the *Sphagnum*, and therefore a matter of physiological interference. When this factor disappears, when the physiological interference is changed, *Chamaedaphne* succeeds the *Sphagnum*. Under the *Chamaedaphne*, *Sphagnum* lives in a very different environment, and the differences are due almost wholly to the physiological interference of the *Chamaedaphne*. The results of this difference are exhibited in the luxuriance of the *Sphagnum*, the reduction or complete disappearance of secondary species of the *Sphagnum* zone, and the appearance of new secondary species which do not extend beyond the *Chamaedaphne*. The conclusion is that the two zones represent two different associations.

On exposed rock beaches crustaceous rock lichens may constitute the entire vegetation. In this case the limitations of the plant life are fixed by a severe environment, strong light, destructive action of storm-waves, and

lack of adequate soil. A typical one-layered association is developed. Above the limit of wave-action soil may accumulate, and a two-layered association of mosses and herbs may develop. Between these two a transition zone is marked by an apparent mixture of the two associations, the former on the exposed rock surfaces, the latter in the crevices, but the two live under radically different environments. The conclusion is that one-layered associations may exist.

I have elsewhere called attention to the importance to synecology of a correct understanding of the two processes, classification and combination. The general difference between them is that classification of concrete units always leads to an abstract concept, while combination of such units leads to another, more complex, concrete unit; an important corollary is that abstract concepts can not be subjected to combination, but only to further classification. Much has been written on the abstract and the concrete in synecology, and much of the maze into which ecologists have been led is due to their failure to grasp the dual nature of most of our ordinary nouns. *Dog*, in common use, is an abstract concept, based on our experience with many individual specimens of *dog* in the concrete.

We must admit that a *stand* of vegetation is a concrete entity. Since it is composed of separate individual unit plants, it must be a combinatory unit. An individual plant is a combinatory unit, composed of the sum of leaves, roots, and stems. A leaf is a combinatory unit, composed of the sum of cells. Now cells can be classified; leaves can be classified, in both cases according to their similarity. We admit the desirability of classifying leaves into opposite and alternate, simple and compound. But who would deny the practicality of continuing the combination-process and recognizing the plant-individual? Individuals can be classified, into species, into vegetation-forms, into economic groups, all of which have a good purpose. But who will deny the great desirabilities of continuing the combination-process with individuals, which results in a *stand*?

In all these examples of combination, dissimilar units are grouped together because of a strong genetic or dynamic relation which binds them together. The new units which are produced by combination are characterized individually by this connection, and separated from each other by a break in the connection, either in degree or in kind. It is illogical for one to attempt to set up a combinatory concrete unit which disregards these two features of close relation of the component elements and of discreteness between the units.

Both of these prerequisites are violated when a *synusia*, at best a very weak concrete unit, is accepted in preference to the *stand* (in its usual sense), where both features are highly developed. A vertical section through a *synusia* may be compared to a chain with very weak links; a similar section through a *stand* to a netting where the strong interconnecting bonds in the vertical direction compensate for the relatively weak lateral unions.

SUMMARY

A synusia is a concrete combinatory vegetational unit, in which the component elements are united by relatively weak genetic and dynamic bonds.

A stand of two or more synusia is a concrete combinatory vegetational unit, in which the component elements are united by relatively strong genetic and dynamic bonds.

The great majority of one-layered stands (lone synusiae) may be explained by temporary suppression, or delayed appearance of other synusiae.

As a unit for the development of the classification concept of the association, the stand has logical advantages over the synusia. Lippmaa's theory is rejected.

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ON THE DEPTH AT WHICH FISH CAN SEE

GEORGE L. CLARKE

*Biological Laboratories, Harvard University, and Woods Hole
Oceanographic Institution*¹

At what maximum depth fish can see in the ocean and in lakes has remained a matter for speculation up to the present time, first because little was known regarding the strength of the illumination at various depths and second because no adequate tests of the sensitivity of the fish eye had been made. During the past 10 years, however, the penetration of daylight into natural waters has been carefully studied by a number of investigators in various parts of the world. Furthermore, the recent excellent work by Grundfest ('32) on the sensibility of the sun-fish, *Lepomis*, gives us a reliable yardstick for one species of fish.

In view of the fact that these two sets of data are now available it occurred to me that it would be of interest to calculate the greatest depth in several different types of water at which the sun-fish could just discern an object of a certain size at a given distance. Although the validity of certain assumptions must be granted in order to make such a calculation, it seems probable that we can arrive at the right order of magnitude for this fish. Whether the photo-sensitivity of other fish is similar to that of *Lepomis* can be decided, of course, only by the performance of suitable experiments. The vision of fish with "telescopic" eyes and of other highly specialized species is undoubtedly on an entirely different scale.²

In the experiments on *Lepomis*, which were carried out for quite another purpose, Grundfest made use of the rheotropic response. The fish to be tested was confined in a cylindrical glass jar around which was placed a cylindrical screen composed of equal and alternate vertical bars and spaces and illuminated to any desired intensity by a band of light, 2 m μ wide, from any part of the spectrum. When this screen was rotated in either direction, the fish responded by a sudden movement in the direction of the rotation, provided that the illumination was above a certain threshold the value of which depended upon the part of the spectrum being used. By repeated trials of

¹ Contribution No. 100.

² A correlation undoubtedly exists between the degree of enlargement or of degeneration of the eyes of deep-sea fish and the depth (and consequently the illumination) at which they live. The issue is confused, however, by important differences which apparently depend upon whether the fish is bottom-living or pelagic and whether or not it possesses light organs. This problem has not yet been satisfactorily elucidated (Murray and Hjort, '12, p. 680).

this sort the spectrum was explored and the spectral sensibility curve determined.

The fact that the sensibility curve for *Lepomis* shows a sharp peak between wave-lengths 530 and 550 $m\mu$ is of interest because it is this general part of the spectrum of daylight which penetrates most effectively into most lakes and into coastal ocean water—the part of the sea in which fish occur in the greatest abundance. The water of the Sargasso Sea, on the other hand, is more transparent to blue light, while in the case of certain lakes and ponds the water contains stains which absorb the shorter wave-lengths so rapidly that the yellow or red component of daylight is found to predominate. H. R. James ('36) has calculated on the basis of laboratory experiments that of the energy of daylight between 300 and 800 $m\mu$ which would reach a depth of 100 meters in distilled water 60 per cent would fall in the blue band and only 23 per cent would be in the green. At the surface 17.7 per cent of the energy is in the blue region and 12.3 per cent in the green. These results raise the question of the possibility of a shift in the sensitivity of the eye of a deep water fish toward the blue end of the spectrum.

In Grundfest's experiments the minimum brightness at which the fish would respond for the 2 $m\mu$ band in the most effective part of the spectrum corresponded to a brightness of 1×10^{-6} millilamberts for white light as judged by the human eye. Although, theoretically, allowance should be made for the relative effectiveness of other parts of the spectrum since in nature the illumination to which the fish is exposed is obviously not confined to a narrow band, this unfortunately cannot readily be done because of the method used to measure brightness. However, it is extremely doubtful that a large correction would be necessary and since we are attempting to find merely the order of magnitude, this difference may be neglected.

The assumption has tacitly been made that when the fish ceases to respond it no longer "sees" the revolving screen. The further question arises of whether the visibility of a series of bars and spaces moving across the field is the same as that of a single object of the same diameter as the width of the bars. Hecht and Wald ('34, p. 520, footnote) found that slow movement, such as was used in all the experiments with this method, does not affect the visual acuity curve in man. Therefore, since the bars were 2 mm. wide and at a distance of 1 cm. from the fish's eye (thus subtending an angle of about 11°), we may assume that the fish could just see under an illumination of 1×10^{-6} millilamberts an object 2 mm. in diameter at a distance of 1 cm., or a 2 cm. object at 10 cm., or a 20 cm. object at 1 meter, and so on.

Since the sun-fish eye is so much more sensitive to radiation between 500 and 600 $m\mu$ than to other regions of the spectrum it is most appropriate to use data for the intensity of submarine irradiation obtained by a photometer, such as one of those employed by Oster and Clarke ('35), with a maximum sensitivity in that region. According to their results the irradiation from 490 to 620 $m\mu$ at the surface of the sea off the coast of Massachusetts during

the middle of a bright day in summer reaches an intensity of about 20,000 $\mu\text{w}/\text{cm}^2$. In the Sargasso Sea the irradiation at the surface was only slightly greater, having a magnitude of about 25,000 $\mu\text{w}/\text{cm}^2$. Now the minimum brightness for the vision of the sun-fish of 1×10^{-6} millilamberts is equivalent to an irradiation of $1 \times 10^{-6} \times 1.5$ microwatts/ $\text{cm}^2 = 1.5 \times 10^{-6}$ $\mu\text{w}/\text{cm}^2$. Since an intensity of 20,000 $\mu\text{w}/\text{cm}^2$ is approximately 10^{10} times this, it is apparent that the fish can see under an illumination of 10^{-10} times the maximum value of daylight—or a reduction of ten logarithmic units. This is approximately the same as for the human eye. The instruments which have been found practicable for light penetration investigations have not been sufficiently sensitive to follow the reduction of light in the water for more than three, or at most four, logarithmic units. However, if we assume that the transparency of the water below the maximum depth reached by the photometer is the same as that in the surface strata, the data may be extrapolated. This assumption is justified, to some extent at least, by the fact that in many cases (and in all the cases considered here) there is no radical change in transparency within the depths actually measured. Accordingly, the approximate depth at which the minimum intensity for vision exists (during the hours of bright daylight at the surface) for each type of water investigated has been calculated by finding the average number of meters of water causing a reduction in intensity of one logarithmic unit and multiplying this value by ten.

In so far as it is reasonable to assume that the vision of our common marine fishes is similar to that of *Lepomis*, which inhabits fresh-water ponds and lakes, the figures in the upper part of table I, based on the data of Oster and Clarke, give the extreme depths at which vision would be possible in different types of water. According to these approximations fish would be able to see objects on the bottom in coastal waters. In the case of localities where the "depth of minimum illumination" is much greater than the depth to the bottom, such as Georges Bank, it appears that vision would be possible for fish during most of the day because the intensity of daylight is within one logarithmic unit of its maximum for several hours before and after noon (Clarke and Oster, '34, fig. 6).

Although taste, smell, and touch are undoubtedly used in certain cases for the location of food, most fishes apparently depend chiefly upon sight (Bigelow and Welsh, '24, p. 416 and p. 451). The general conclusion that vision is possible for fish on the bottom in coastal waters is supported by the following observation made by Mr. R. A. Nesbit of the United States Bureau of Fisheries. Mr. Nesbit found that white hake which he took in a bottom trawl at a depth of 132–154 m. off Bodie Island, North Carolina, were gorged with butterfish and other small active fish which presumably the hake could not have caught unless they had been able to see at that depth.

In order to compare these data on fishes with the ability of divers to see under water, I made inquiries of Mr. H. V. Greenough who had been working

with conventional diving equipment on a wreck in 29 m. of water in Vineyard Sound about five miles distance from the point off Gay Head where Oster and Clarke had made measurements. Mr. Greenough told me that at that depth tools could be clearly seen at arm's length during several hours in the middle of bright days in July. On one occasion sufficient light existed to permit work on the wreck to continue until 7 o'clock in the evening.

The value arrived at for the Sargasso Sea of 430 meters is of interest in comparison with Beebe's observation from the Bathysphere that complete darkness for the human eye was reached at a depth of between 520 and 580 m. Dr. Beebe has informed me (private communication) that without artificial illumination he was able to see a non-luminous fish four inches long (*Cubi-ceps*) at a depth of 210 m., a shark at 240 m., and a jelly-fish (*Aurelia*) at 350 m. although entangled luminescent organisms may have aided vision in the last case. In another part of the Sargasso Sea, Helland-Hansen ('31) found that a highly sensitive photographic plate was slightly blackened after an exposure of 80 min. at a depth of 1000 meters. If we assume that a deep sea fish can see as well in blue light as *Lepomis* can in green light, then the maximum depth for vision in the Sargasso Sea would be about 750 meters since an average of 75 m. of this type of water are required for a reduction of one logarithmic unit in the blue region of the spectrum (Clarke, '33).

The depths for the limit of vision for the sun-fish have been similarly calculated for three of the large number of lakes in northern Wisconsin whose transparencies have been carefully studied by Birge and Juday ('31, '32) and for one lake in Minnesota investigated by Erikson ('33), although the different methods used in the measurement of light penetration make comparisons difficult. The values arrived at for these four lakes are set forth in the lower part of table I. Data on the depth at which the energy is reduced to 10 per cent of its surface value for a large number of other lakes are available from the laboratory measurements of James ('36). Crystal Lake is the clearest of all those investigated and Adelaide Lake is one of the most

TABLE I. *Maximum depth for vision of fish similar to Lepomis in various types of water*

Types of water	Thickness of stratum causing reduction of 1 log unit	Depth of minimum illumination for vision of fish similar to <i>Lepomis</i> (10 × column 1)	Depth of water to the bottom
Deep Basin of Gulf of Maine	23 meters	230 meters	165 meters
Georges Bank	18	180	60
Woods Hole Harbor	7.5	75	20
Off Gay Head	13	130	30
Sargasso Sea	43	430	4500
Crystal Lake, Wisconsin	11	110	21
Adelaide Lake, Wisconsin	2.8	28	22
Trout Lake, Wisconsin	6	60	35
Gunflint Lake, Minnesota	7	70	50

turbid with the exception of those which are deeply stained. Trout Lake is the deepest of the Wisconsin lakes studied. In all of these and even in Gunflint Lake which is still deeper, the calculations indicate that, just as in coastal waters, vision would be possible for fish similar to *Lepomis* all the way to the bottom.

SUMMARY

It has been calculated from the data of Grundfest ('32) and Oster and Clarke ('35) that the minimum illumination for vision for the sun-fish, *Lepomis*, is approximately 10^{-10} times the maximum value of daylight. The depth at which daylight would suffer a corresponding reduction in different types of ocean water and lake water has been found by extrapolating from existing measurements. The results indicate that for fish whose visual sensitivity is similar to that of *Lepomis* vision would be possible at the bottom in coastal regions and in lakes and at a depth of at least 430 m. in the Sargasso Sea.

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TREE RING WIDTH AS AN INDEX OF PHYSIOLOGICAL DRYNESS IN NEW ENGLAND

CHARLES J. LYON

Dartmouth College, Hanover, N. H.

The use of tree ring width as a measure of relative secondary growth rates and growing conditions has received little attention in New England or any other humid section of the United States. Analyses covering short periods of time, dealing with a few trees only and often with several species in the same study, have led to contradictory and poorly supported conclusions, in sharp contrast with the extensive data and dependable conclusions from studies in the southwestern states. Since the humid regions lack any such obvious factor for control of growth as the long droughts of relatively dry regions, it has remained an open question whether rainfall or any other factor, or simple set of factors, controls the growth rates of trees in well-watered areas. This paper presents the results of an intensive study of the relations of growth to climate shown by the eastern hemlock, *Tsuga canadensis*, in northern New England.

The critical use of annual rings as measures of radial growth rates in response to environment requires (a) measurements sufficient in number and accuracy really to represent growth, and (b) use of the data for each tree with constant appreciation that they involve responses of a living organism to many factors internal and external, even though one or more factors may dominate. This means especially that more pronounced effects should be expected when the dominant factor is quantitatively much below normal than when it offers a relatively favorable opportunity for growth; for under these most favorable conditions the full and precise response of the tree may be prevented by a deficiency of even one other essential factor. Likewise, so much allowance must be made for interplay of factors when the dominant one is quantitatively not far from its average value, that the practical approach to the problem is to notice the responses to extreme values of the factor suspected of being outstanding in its control of growth rate.

It is understood that such control may be either direct or indirect or both, in view of the many interrelated factors of temperature, evaporation, distribution of rainfall from day to day, soil texture and profile, root distribution, interception of rainfall by tree crowns, etc. Failure to allow for contributing factors like these, which all workers must admit as important, has led some writers to expect or require nearly perfect correlations under all conditions. Thus, Adams ('35, p. 22) concludes that Robbins ('21)

"failed to find a consistent correlation between the ring width of oak and precipitation" when this worker was actually able to express the growth relations by such an exact formula, involving temperature and precipitation, that the "sums of the observed and calculated values for the 30 years differ by less than 5 per cent." Adams himself ('28) in a 10-year analysis of very young Jack pine, *Pinus banksiana*, grown in evenly spaced plantings, decided that his annual diameter measurements with calipers outside the bark, proved that "under Vermont climatic conditions temperature differences do not seem materially to affect diameter growth unless coincidentally differences occur in the amount of rainfall" (p. 44). In his summary of the same work, Adams also concluded (p. 2) that "Rainfall during the spring months (March-June) directly affects the width of the growth ring provided there is no root competition." Since the statistical basis for these conclusions appears only in two separate tables (p. 17 and p. 43), it is not clear how these positive correlations were arrived at, unless through simple inspection. In fact, Adams implies as much by his statement (p. 43) that "graphical or mathematical representations do not readily show the facts" concerning such correlations. In other words, a fair degree of positive correlation is significant in this field of study, especially since a complete response to a climatic factor may be delayed for one reason or another.

Finally, it should be noted that correlations established between variables over a period of many years are probably more significant than equally good or better correlations over a space of relatively few years. In the analysis of tree ring widths and their dependence upon climatic factors controlling tree growth, this principle emphasizes the need for using long records of growth rates from mature trees. Even a few such records from trees at least 100 years old are usually more valuable than a large number of measurements from young trees or from the last few rings as sampled by an increment borer, though the last method may give significant results if the responses to external factors are very distinct.

REVIEW OF PREVIOUS WORK

With these basic principles in mind, it is not difficult to understand the lack of agreement and decision in most of the work thus far reported for eastern United States. Except for the recent work of Diller ('35) with beech in northern Indiana, no thorough analysis has been attempted and some of the reports commonly cited are brief notes of almost casual observations made with a few trees or for only a small number of years.

The only studies actually made in New England have been those of Douglass ('19) and Marshall ('27) with hemlock and Burns ('29) and Adams ('28) with pine. Their published conclusions range from no correlation with rainfall to an "unquestionable" positive correlation with annual rainfall of the calendar year.

Douglass ('19) took measurements from two stands of old hemlock trees near Windsor, Vermont and reported the average ring widths of 11 trees by means of a single graph. The measurements were made at stump height along a single radius for each tree. In spite of his previous experience with tree rings as indicators of climatic factors, and even though the individual graphs showed many cases of pronounced maxima and minima in certain years over a period of more than 250 years, Douglass was unable to find a constant relationship between growth rates at Windsor and rainfall of the region as measured at Hanover and Concord, N. H. However, his data have been successfully incorporated into the present study of an adjoining area and the difficulty seems to have been due to use of annual rainfall records from stations with slightly different rainfall distribution.

Marshall's work ('27) with hemlock was done on a plot of a few acres in northern Massachusetts. Unfortunately for exact comparison with the findings of others, his analysis was made with decadals instead of annual amounts of growth and precipitation. In spite of the resultant possible masking of moisture effects, Marshall did obtain a very positive correlation between 10-year summations of annual rainfall and the decadal increments of trees which grew on ten sandy, well drained sites. The correlation coefficient was $.70 \pm .04$. For seven poorly drained sites, the correlation coefficient was $-.06 \pm .09$ and therefore indicative of no relationship. The analysis of the dry site trees was further broken down to include comparison of trees growing under various degrees of suppression. The result was highest correlation with suppressed trees and next highest with dominant trees, showing that rainfall effects appear distinctly in hemlock rings in spite of great differences in root and crown development of individual trees, provided they do not grow on sites possessing reserves of ground water.

The work done with pine in New England is limited to short studies of young trees at Burlington, Vermont. Adams ('28) used *Pinus banksiana* and his results have already been cited. They indicate some correlation between spring rainfall and radial growth although a temperature effect also appears to be shown at the same time. Measurements were made for only 10 years and his work as a whole was directed toward effects of tree spacing, with the relations to climatic factors an incidental consideration.

Burns ('29) considered the growth increments of various species for an 11-year period but only made measurements of trunk diameters at the start and close of the period. He likewise considered only the sum of the rainfall for the 11 years. His conclusions appear to be based chiefly on results with white pine and are covered by his statement (p. 2) "There can be no direct correlation between rainfall and diameter growth." Since the general method of attack in this work was computation of total precipitation per inch of wood formed along a diameter, without annual measurements of growth rate, the results are hardly comparable with those of other workers.

Of the studies made with tree rings at a distance from New England, those in the northern tier of states are more nearly comparable. Although the careful study of Robbins ('21) in Missouri gave clear-cut results, the trees were oaks and the general moisture relations are very different in that state and with a type of tree more characteristic of warmer, drier areas. Likewise, the recent work of Lodewick ('30) with longleaf pine in Florida is not comparable because of radically different climatic relations. However, it is interesting that this species does show a dependence of its radial growth upon seasonal rainfall.

Observations made in Michigan by Bogue ('05) are frequently cited but should not be rated highly except as a pioneer effort. The period of years used was only 13 and the 42 stumps measured were of 15 species. The conclusion that rainfall effects are recorded in the following season of growth was based on a few cases of very low or high annual rainfall.

The brief note by Stewart ('13) concerned his measurements on the stump of a single oak tree but he appears to have made the most of his data for a period of 70 years. His decision to credit the rainfall of June and July with a controlling influence in that part of western New York, is quite in accord with his data. He could not find a good correlation with temperatures, such as Brown ('15) found for white pine in central New York, but the radial growth of the pine could not be correlated with rainfall in that region.

The first study to be reported for beech, *Fagus grandifolia*, was the thorough analysis by Diller ('35) who used a 21-year period and the increment borer method with mature, dominant trees. Mean data were obtained from 70 trees in 7 woodlands of northern Indiana. His parallel graphs of growth increments, rainfall and mean temperatures support his conclusion that radial growth usually varies inversely with June temperatures and directly with June precipitation. There were a few cases of a lag of one year in the rainfall relations. This situation was checked and in each case found to be caused by an accumulated soil moisture deficiency from the drought of the preceding year or years. Because of these lag effects, it was "practically impossible to correlate statistically the relation between rainfall and growth," even though the direct relationship was apparent. However, it must be pointed out that these beech trees were growing near the western edge of their range. The climatic relations with growth increments there may not be comparable with the same relations in the northeastern states.

MATERIALS AND METHODS

The hemlock trees for this study grew in six scattered woodlands of eastern Vermont and a mid-belt across New Hampshire. In figure 1 the sites are located and named by the towns in which they occur. The habitat of the Windsor trees cannot be described because their measurements were made by Douglass. The location and nature of the other sites are as follows:

Benton.—The 9 trees used were scattered through about 3 acres of mixed forest at an elevation of 1800 feet. The land had a gentle slope to the west but was not perfectly drained because of terraces. A third of the trees were rooted in ground affected by a typical mountain spring with a small flow of water.

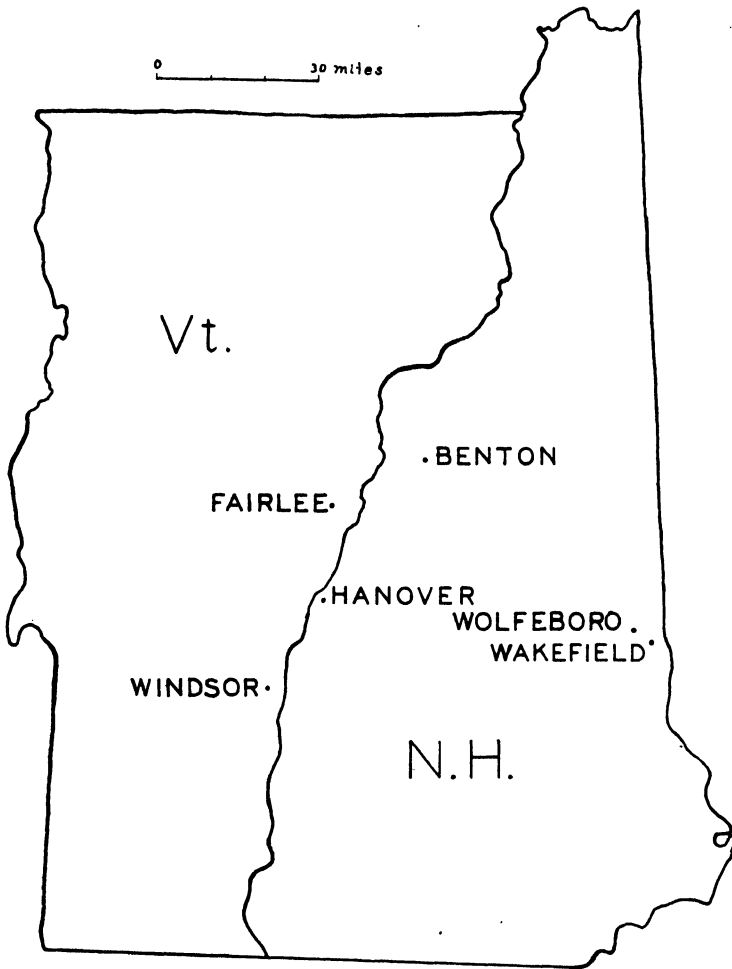


FIG. 1. Map of Vermont and New Hampshire, showing the locations of the six forest sites from which tree sections were obtained.

Fairlee.—Three tall trees were sectioned from each of two mixed forests about 2 miles apart in the town of West Fairlee, Vt. Both sites were on sloping land, one toward the east at an elevation of 800, the other toward the northwest at 1500 feet. The trees grew in good but stony soil on tracts more nearly level than the average slope of the sites which have been handled as one because of the short distance apart and especially since the individual trees gave growth rate curves with nearly identical maxima and minima. To have

handled them as separate groups would not have altered the results and conclusions.

Hanover.—This site was a wood-lot with a rough terrain of ridges and hollows at an elevation of about 700 feet. The airline distance to the weather bureau cooperating station at Dartmouth College is about 2 miles, without appreciable difference in altitude. The eight trees were located within an area of a few acres but with all ranges of habitat from low ridge crest to the margin of a summer-dry swampy trough. Unlike the other sites, the area appeared to have been the scene of selected cuttings of trees at various intervals during the 19th century, so that the dates of release of the small hemlocks were not the same for any two trees sectioned for this study.

Wakefield.—All of the 7 tree stumps sectioned at this site were distributed along a low ridge in a rolling wood-lot at an elevation of 700 feet. The summer water table could not have been unusually low because a low trough roughly parallel to the ridge was unpleasantly wet in mid-August. The area about the site is one of low hills across Lake Winnepesaukee from Lakeport, the nearest station with a long period of weather records.

Wolfboro.—The six trees at this site grew on low, rough land near an inland lake and a stream flowing into it. These trees and many others had formed a close, nearly even-aged stand which had been released in 1794–95, following severe suppression for many decades. The site is only 5 miles from the Wakefield area but at a lower elevation (600 ft.) and with a deeper soil and probably higher water table. The sections were cut from the best preserved stumps which had weathered for 10 years before the unrotted tops were removed for ring analysis.

For these five sites, the data and results to be described have been obtained by the methods outlined in a preliminary paper (Lyon, '35). They will be re-stated briefly, with particular reference to precautions taken to avoid errors and to obtain unprejudiced data which bears no sign of selection except as the tree stumps were chosen for maximum age, unrotted centers and avoidance of extremes of habitat and competition with other trees within the sites represented.

For each group of trees, thin cross sections of the trunks were cut, above the level of marked buttress flares in practically every case. The sections were taken to the laboratory and the exact widths of annual rings were measured along three average radii each, by means of a 10-power dissecting binocular with a graduated measure in one ocular. The mean of the three measurements was taken as an index of the relative growth rate for the year. The unit on the scale in the ocular was equivalent to 0.1 mm. but all data are reported in millimeters.

The regularity of ring formation was constantly checked by comparison of the count along each radius at intervals of 50–75 years as well as at the last ring formed. A few cases of false rings were detected and eliminated by these checks but the greater number of errors discovered were due to failure

of rings to form along all radii (wedged-out rings). This irregularity is not uncommon during severe suppression, particularly during years when relatively narrower rings are due to some climatic or nutritive effect. For such cases, a zero width was tabulated and the resulting average gave a very narrow ring in a group already too narrow even to be counted without magnification.

A total of 36 tree sections have been cut and analyzed completely, requiring over 27,000 individual measurements and the calculation of about 10,000 averages. The widths were taken to the nearest .05 mm. for rings over this dimension; narrower rings were recorded down to .01 mm. with some loss in accuracy but with relative values correctly stated. To make narrow rings visible, it was only necessary to apply a light oil (usually paraffin oil) before or after removing a very thin slice with a sharp razor blade held in the fingers and grasped at both ends, the cutting operation performed in the illuminated field of view of the binocular. Sections with 100 rings to the inch were not uncommon but for all our data no allowance need be made for accuracy of count and therefore of dating.

The average age of the trees was 279 years and only one section had less than 200 rings. Likewise with the exception of one tree, it was possible to measure every ring from pith to bark. There were 5 sections with more than 350 rings each, the maximum being 391.

One very old tree was analyzed completely at two levels before the duplication was known. Either set of measurements could have been used without perceptibly altering the sequence of highs and lows in the curve, so all six radii were averaged as though measured at one level. If on the contrary, as some writers stress (Adams, '28; Burns, '29), there are decided variations in the width of a given ring at different levels in the trunk, this condition has been allowed to influence our data for the other trees and the results have been obtained in spite of it.

RESULTS

In connection with the data, shown in the form of annual growth increments plotted against calendar years of their production, it can be said that *all* measurements have been included, even though a better case could have been made out by omitting the data from a few trees which did not appear to reflect climatic influence as precisely as did the other trees. Because of the great variations in forest sites used and particular habitats represented by the individual trees, it is urged that the entire set of data forms an unprejudiced statement of growth rate sequences in northern New England forests for more than three centuries.

The first point to be demonstrated is the degree to which individual trees in a group were alike in their responses to their environment, year by year. This will be referred to as cross-identification, since an established series of dated maxima and especially of dated minima enable one to identify the year

of growth of any ring in a sequence of measured but undated rings. In figure 2 are shown the graphs of the five oldest sections from the Wolfeboro site. The graphs have been plotted in a vertical series and as close together as possible without overlapping. The scale of ring widths (indicated for the oldest tree only) was chosen with reference to the accuracy of the measurements and ease of noting the cases of cross-identification.

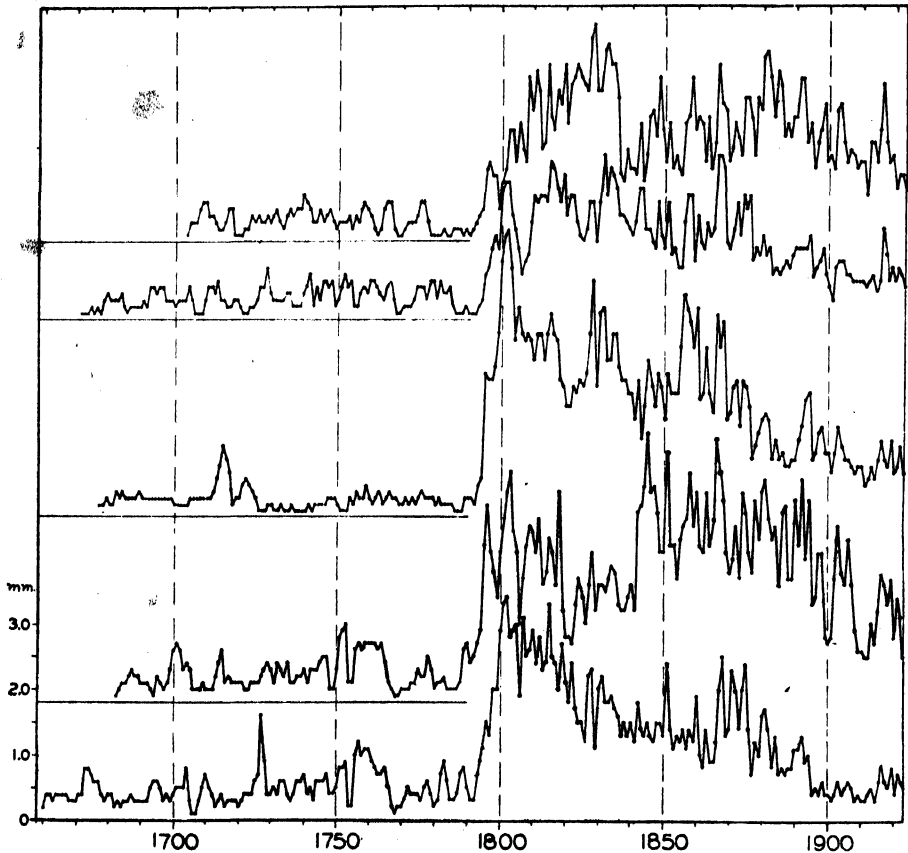


FIG. 2. Cross-identification between the five oldest trees from Wolfeboro, N. H. Calendar years on the horizontal axis; mean widths of annual rings on the vertical axis. The base line indicated for the early years of each of the four upper graphs represents zero width of ring in each case.

The degree of cross-identification between these five trees is typical of all groups studied. Instances of perfect agreement in having rings relatively narrower than the preceding and following year will be found for 1755, 1769, 1813, 1826, 1870, 1877, 1895, 1911, and 1914. In the same way, relatively wide rings characterize the years 1789, 1831, 1851, 1898, and 1916. Many other years show marked agreement, kept from perfection by the usual biological variations among individual plants and animals.

In order to show that this degree of agreement is significant in being well above the workings of chance, the period of 1800 to 1850 has been used for a detailed analysis of correlation in the upward and downward fluctuations of the five graphs. This particular half-century was selected only for purposes of comparison with a like analysis of correlations between all sites used. The method has not even been applied to any other period or single group of trees because it only shows in concise form the correlations which are obvious from inspection.

Briefly, the method (suggested by Huntington) consisted in tallying for each change from year to year, the nature of the fluctuations by means of the symbols +, —, and 0. If all 5 curves went up together, as they did in 1801 for example, the tally sheet showed a row of 5 +'s. A similar row of — signs indicated perfect agreement in a smaller growth increment in all 5 trees for a given year, such as 1806 and 1836. Instances of no change in ring width were infrequent.

The result of this analysis for the years 1801–1850 was 5 cases of 5 +'s and 7 cases of 5 —'s, making a total of 12 perfect correlations out of a possible 50. The law of probability allows for such correlation in only 1 year out of 16, disregarding the effects of the 0 symbol. The difference appears to be highly significant and to show that individual trees do respond essentially alike in the same forest, due allowance being made for the years in which the dominant factors of the environment are quantitatively so near their mean values that the effects of other independent variables give different results in one or more of the five individual trees.

Comparison of the radial growth rates for the six woodlands shown in figure 1, is possible through the six graphs in figure 3. Each curve represents the mean growth increments for the site indicated by name. Since the trees were of different ages and cut in various years, these graphs of mean values for each year the trees lived do not all start and end together.

The major changes in level of these graphs reflect a fact well known to those familiar with hemlock trees—the “suppression” of growth and the “release” following defoliation or removal of larger, nearby trees. The resultant upward trends in growth rate do not concern the present analysis of growth effects except that they sometimes mask the climatic effects during the period of increasing growth rates just after release. Also during the period of suppression the variations in climatic factors are probably not registered with great fidelity but this feature in the life history of most hemlock trees cannot be avoided. Our results have been obtained in spite of these major differences in growth rates, through constant use of relative as opposed to absolute growth increments. Thus a “narrow” ring formed some time after release may be much wider than a “wide” ring formed during suppression. This usage also prevents the adoption of dot diagrams and similar graphic methods for analysis of correlations between our graphs or between

growth rates and any climatic factor, such as rainfall; such methods depend upon relations between absolute values.

By simple inspection, it is clear from figure 3 that the curves for the six sites (the data from Windsor being that of Douglass ('19) as published in graphic form) show about the same degree of cross-identification as the curves of individual trees in figure 2. Striking cases of lows and highs in

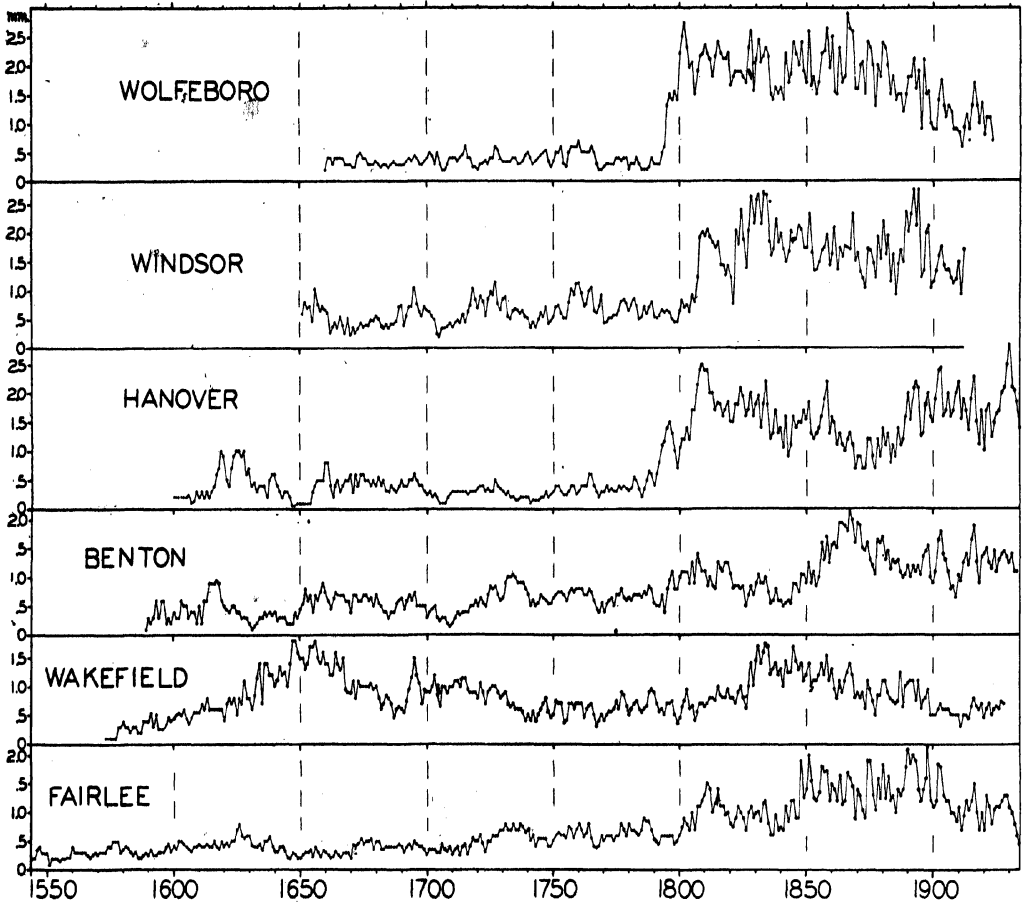


FIG. 3. Cross-identification between groups of trees from the six woodlands located in figure 1. Mean ring widths on vertical axis; calendar years on horizontal axis. Each graph represents mean growth increments of all trees sectioned at the site indicated by name.

all curves can be found. A few such are 1695, 1705, 1851, 1900 and 1916. The agreement is particularly remarkable in view of the great differences in sites and attendant climatic factors. Although all sites are included within a circle of 40 mile radius, there are important differences in soils, exposure, temperatures and temperature ranges, annual rainfall, etc. due to various differences in topography of the area and distances of the sites from the Atlantic Ocean.

To express the degree of correlation between the six curves, as was done for the five graphs of figure 2, the same method was used for the same period—1800–1850. Since there is one more graph in figure 3, the probability for chance agreement is less and will account for only 1 perfect correlation in 32 years. The total cases of perfect correlation actually numbered 21 for the 50 years. Of these, 10 showed 6 +’s and 11 showed 6 —’s while 10 other cases had 5 alike. There were at least 4 alike in 80 per cent of the years, still disregarding the effects of the 0 symbol, the use of which tends to decrease the chances of correlation in all these comparisons. These figures show that the means for groups of trees in six scattered woodlands give even better cross-identification than individual trees in the same forest. The percentages of perfect agreement is nearly twice as great for group averages as for single trees, perhaps through the elimination of individual variations in the comparisons between groups of trees.

Because the specific years with relatively narrow or wide rings are of especial interest in any attempt to determine why the average growth rates should have been retarded or favored in those years, a list of them is shown in table I. Entries have been made only when essentially the same date was marked by a maximum or minimum at two-thirds or more of the sites. For any one site, there are a few other marked maxima and minima as one would expect. Because of lack of dependable data previous to 1600, no entries were made for the 16th century although a few can be found by inspection of figure 3. The occasional instances of a year’s difference between the entries for years with either narrow or wide rings, such as 1764–65 or 1849–50, will be considered later; they seem to be due to differences in soil moisture reserves at the several woodland sites.

As a further check on the accuracy and importance of this series of dates and the corresponding favorable and unfavorable seasons for radial growth of trees, a weighted average curve was constructed from the data used for the six individual graphs, up to 1800. The values were so weighted as to avoid the undue effects of differences in absolute values, such as between Fairlee and Wakefield for example. Such a curve was not attempted for the period after 1800 because of the complications due to eventual release of most of the trees. Since the graph of weighted averages merely confirms table I in practically every detail, it is not reproduced here. Because the table of dates shows even greater consistency after 1800 than before, it is felt that the agreement between groups of trees at different New England sites has been sufficiently indicated.

DISCUSSION

Since the measurements of annual growth increments were taken from 47 trees and 6 sites selected only by their availability, it is felt that the only possible factors which could have acted simultaneously to affect the growth

rates are those which determine the general climate of the entire area. Of these, the only ones available for separate, detailed analysis in a search for correlations with growth increments, year by year, are temperature, precipitation and possibly solar radiation. At best these attempts at correlations between growth indices and estimates or measurements of climatic factors are limited to consideration of relatively recent times, particularly in northern New England. Much of the area was in the pioneer stage until late in the 18th century while its modern records of climatic factors go back only 100 years at the most, and are still kept at only a few stations. It will therefore be impossible to make accurate comparisons between growth and climate for all our sites.

The only definite records of solar radiation are contained in such phrases

TABLE I. *Cross-Identification of New England Hemlocks*

Narrow Rings						Wide Rings					
Benton	Fairlee	Hanover	Wakefield	Wolfeboro	Windsor	Benton	Fairlee	Hanover	Wakefield	Wolfeboro	Windsor
1606	1606 07	1607	1606	No data	No data		1613	1613	1613	No data	No data
1622	1622	1622									
1631		1631	1631								
1645	1645		1645								
46	46										
1655	1655				1655		1656		1656		1656
1657	1658		1658		1658	1659	1659	1660	1659		1659
1662	1662	1663	1662	1663	1662		60				
			63								
1670	1670	1671	1669	1671	1670						
			70	72		1680	1680	1681	1680	1680	1680
1691	1691	1691	1691		1691						
		92				1695	1695	1695	1695	1695	1695
1705	1704	1705	1705	1706	1705						
	05	06		07							
		07									
1720			1720	1720	1720						
1723	1723	1723	1723		1723	1727		1727	1726	1727	1727
1741	1741	1741	1741	1742	1741				27		
1743	1743		1743	1743	1743			1747	1747	1747	1747
1748	1748	1748	1749	1749	1748						
49					49	1752	1752	1751	1751	1751	1751
1754	1754	1754	1754	1754	1754	53		52	52	52	52
55	55	55	55	55	55				53	53	
1762	1762		1762		1762						
63					63	1764	1764	1764	1765	1765	1765
1767	1767	1768	1767	1768	1767			65			
68	68			69							
1770	1770		1770		1770						
1779	1779	1780	1780	1780	1780	1788	1786	1788	1789	1789	1789
						89	87	89			
1798	1798	1799	1799	1799	1798		88				
99					99						
1804	1804	1804	1804	1804	1804						
1806	1806		1806	1806	1806						
1821	1821	1820	1822	1820	1821						
		21			21						

TABLE I (Continued)

Narrow Rings						Wide Rings					
Ben- ton	Fair- lee	Han- over	Wake- field	Wolfe- boro	Wind- sor	Ben- ton	Fair- lee	Han- over	Wake- field	Wolfe- boro	Wind- sor
1826	1826	1826	1826	1826	1826	1828	1828	1828	1828	1828	1828
1829	1829	1829	1829	1829	1829	1831	1831	1831	1831	1831	1831
1832	1832	1832	1832	1832	1832						
33											
1836	1836	1836	1836	1836	1836	1838	1838	1838	1838	1838	1838
	37			37							
1841	1841	1841	1841	1841	1842	1845	1844	1845	1845	1845	1844
							45				
1850	1849	1850	1849	1850	1849						
					50	1851	1851	1851	1851	1851	1851
1854	1854	1853		1854	1853						
					54	1858	1858	1858	1858	1858	1858
1859	1859	1859	1859	1859	1859						
1862	1862	1862	1862	1862	1862	1867	1866	1866	1867	1866	1868
							67	67		67	
1869	1869	1869	1869	1869	1869					68	
				70							
1873	1873	1872	1873	1873	1873	1874	1874	1874	1874	1874	1874
		73					75	75			
1877	1877	1877	1877	1877	1877	1880	1880	1880	1880	1880	1880
									81		
1885	1885	1885	1885	1885	1885	1892	1892	1892	1891	1892	1892
								93	92		
1895	1895	1895	1895	1895	1895	1894		94	1894	1894	1894
						1898	1898	1898	1898	1898	1898
1900	1900	1900	1899	1900	1899						
			1900	01	1900	1903	1902	1902	1903	1903	1903
			01				03	03			
1911	1911	1911	1911	1911	1911						
1914	1914	1914	1914	1914		1916	1916	1916	1916	1916	
1918	1918	1918	1918	1918							
	1920	1920	1920	1920	No data	1921	1921	1921	1922	1921	No data
								22		22	
1923	1923	1923	1923	1923		1928	1928	1929	No data	No data	
							29				
No data	1934	1934	No data	No data							

as "fair" or "partly cloudy" and these describe conditions only at the hours when observations are recorded. From them it is impossible to obtain a fair approximation of monthly or seasonal sunshine quantities that can be compared with growth increments, either alone or in connection with other factors.

The temperature factor is very complex in relation to plant life because it has so many direct and indirect effects upon vital processes. Practically the only temperature index available for comparison with that of growth rate is the daily mean temperature. It is commonly calculated and reported by calendar months and has been used by other workers in their efforts to establish correlations with growth rates. Using records taken from stations near some of our sites, we have looked in vain for consistent relationships

with hemlock growth rates. In some instances it is evident that temperature conditions have aggravated or modified drought effects while in the presence of large amounts of water a relatively high temperature is often associated with wide rings. In general, the indicated relations with growth are decidedly contradictory.

It is with rainfall that we have found a definite relationship but it is not the simple correlation reported in our earlier papers (Lyon, '35 and '35a). Then it appeared from the first few trees studied that the rainfall of the growing season was the determining factor; we have since found that this holds true only part of the time because a deficiency or an abundance of soil moisture may often be due to the precipitation of the preceding snowless period. This is the lag effect noticed by others (Bogue, '05; Diller, '35) and easy to understand. The relationship as a whole is difficult to demonstrate, however, because a drought or a period of heavy rainfall may affect the trees of one site at once but not be shown at another site until a year later. Inland forests on inclined sites seem to lack reserves of soil moisture in comparison with low sites nearer the coast.

Of the six woodlands represented in figure 3, it is possible to make the best comparison of growth and rainfall for the Hanover site. It is near the Dartmouth College station which has a long record of precipitation quantities. Several possible combinations of its data were assembled and compared with the sequence of mean growth rates shown by the Hanover trees. The significant relationships are shown in figure 4 and table II.

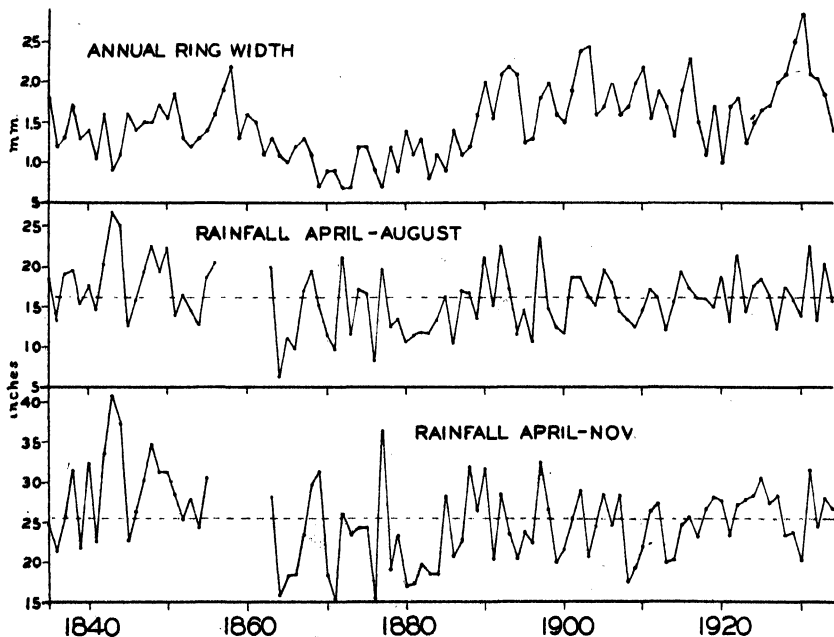


FIG. 4. Growth rates for hemlock (upper graph) and seasonal rainfall at Hanover, N. H. Correlations for critical years are shown in table II. Rainfall data not recorded for the years 1856-1862. Dotted lines show mean rainfall for the periods indicated.

TABLE II. *Growth—rainfall correlations at Hanover, New Hampshire*

Relative Growth	Year	April-August	Preceding Apr.-Aug.	June	Preceding Sept. - November	Apr.-Aug. + Preceding Sept.-Nov.	Preceding Apr.-Nov.
-	1836	+	-	-	+	+	-
+	1838	+	-	+	-	+	-
-	1841	+	+	+	-	-	-
+	1845	-	+	-	+	-	+
(-)	1850	-	+	-	-	-	-
+	1851	-	+	-	-	-	+
-	1853	+	-	+	+	+	-
+	1867	+	-	+	-	+	-
-	1869	+	-	-	-	-	-
-	1872	-	+	-	+	-	+
-	1873	+	-	+	+	+	-
+	1874	+	-	+	+	+	-
+	1875	+	+	+	-	+	+
-	1877	-	+	-	+	-	+
(+)	1880	-	-	-	+	+	-
-	1885	-	+	+	+	-	+
+	1892	+	-	+	-	+	-
+	1894	-	+	-	-	-	-
-	1895	+	+	-	+	+	+
+	1898	-	+	+	-	-	+
-	1900	+	-	+	+	+	+
+	1902	+	+	+	-	+	+
+	1903	+	+	+	+	+	+
-	1911	-	+	-	+	-	+
-	1914	+	+	+	+	-	+
+	1916	+	+	+	-	-	-
-	1918	+	+	-	+	+	+
-	1920	-	+	+	-	-	-
+	1921	-	+	-	-	-	+
+	1922	+	-	+	+	+	-
-	1923	+	-	+	+	+	-
-	1934	+	-	-	+	+	-
		20-12	19-13	18-14	18-14	17-15	15-17

The April-August period was first chosen because frozen ground through March prevents earlier precipitation from affecting soil moisture to any important extent. September rainfall was not added in with the "summer" precipitation because the best evidence available (Lodewick, '28) indicates practical cessation of growth of conifers during this month. The April-November period represents the normal season of unfrozen soil and therefore of a minimum of run-off water. The inclusion of this data in figure 4 is made necessary by the lag effect which is frequently found in the Hanover trees.

Since the usual simple methods of statistical analysis cannot be applied to this mixed relationship between rainfall and relative growth, the correlations between the three graphs of figure 4 are shown in table II, together with a few other relationships which might be thought to hold. The "fall rains" effect is indicated in the September-November column while use of the June data was first suggested by the conclusions of Diller ('35) already described. The dates used in this analysis were taken from the Hanover columns in

table I. They include all critical years for the area under investigation, during the period covered by the broken record of rainfall at Hanover. The term "critical" is used here with reference to the years in which the moisture effects are not masked by other factors because moisture seems to be definitely abundant or deficient in these years. Other possible critical years for the Hanover trees alone were omitted from consideration in order to obtain unprejudiced proof of the growth-rainfall relationship. The correlations for these other years can be estimated by inspection of figure 4.

In table II, the correlations between the relative growth rate (column 1) and the total precipitation are indicated as either positive or negative. They were judged to be positive only if the precipitation followed the ring width in showing a maximum or minimum in the same year or, in some cases, in being far above or below the mean value. The figures at the foot of each precipitation column summarize the ratios between the positive and negative correlations with the first number always the sum of the positive signs in the column above it.

From this table it can be seen that the rainfall of the April–August period gives the best correlation with the growth rate. Most of the other periods also show some positive relationship while the precipitation of the preceding year's snowless period (last column) alone shows more negative than positive correlations. However, this same column is next most important to the April–August column in providing a good explanation for each maximum and minimum growth rate. A positive correlation here means a lag effect in the growth response. That this lag effect is not the general rule is indicated by the preponderance of negative correlations but, taken in conjunction with the first column (April–August), it provides an almost perfect accounting for the 32 critical years in the century covered by the table. With the exception of the years 1850, 1880, 1894 and 1920, this lag effect accounts for the 12 years in which the growth rate does not correspond with the rainfall of the growing season.

The relatively large or small growth of the four exceptional years can readily be understood from other correlations shown in the table. In 1850, 1894 and 1920 the rainfall of the preceding growing season was correspondingly large or small. This is only another type of lag effect, due to storage of moisture in the ground or possibly of food materials in the tree. In 1880 it is obvious that the rains of the preceding fall, either alone or along with the rainfall of its own growing season, gave the optimum moisture supply for a relatively wide ring. Moreover, for 2 of these 4 years (1850 and 1880) the difference in ring width at Hanover was small, as indicated by the parentheses about the symbols for relative growth rate for those years.

This same correlation study was made for the Wakefield site and the precipitation of that locality as measured at Lakeport. Figure 5 shows the relations graphically, year by year, while the correlations for the critical years appear in table III. The conclusions are essentially the same as for Hanover

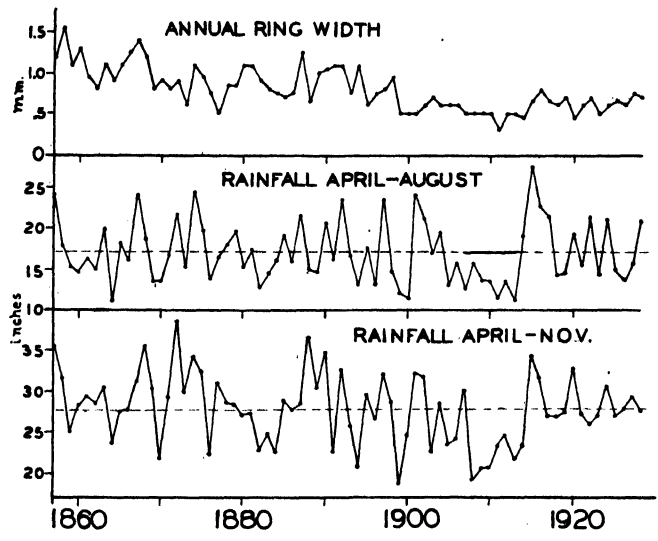


FIG. 5. Growth rates for hemlock (upper graph) at Wakefield, N. H., compared with seasonal rainfall at Lakeport, N. H., 20 miles west of the woodland site. Correlations for critical years are shown in table III. Dotted lines show mean rainfall for the periods indicated.

TABLE III. *Growth—rainfall correlations at Wakefield, New Hampshire*

Relative Growth	Year	April-August	Preceding Apr.-Aug.	June	Preceding Sept.-November	Apr.-Aug. + Preceding Sept.-Nov.	Preceding Apr.-Nov.
+	1858	—	+	—	+	—	+
—	1859	+	—	—	—	—	+
—	1862	+	—	—	—	—	—
+	1867	+	—	—	+	+	—
—	1869	+	—	+	—	+	—
—	1873	+	—	+	—	—	—
+	1874	+	—	—	+	+	—
—	1877	+	+	+	+	+	+
+	1880	—	+	—	—	—	+
+	1881	+	—	—	+	+	—
—	1885	—	+	+	+	+	+
+	1891	—	+	—	+	+	+
+	1892	+	—	+	—	+	—
+	1894	—	—	—	—	—	—
—	1895	—	+	+	+	+	+
+	1898	—	+	—	—	—	+
—	1899	+	+	+	—	+	—
—	1900	+	+	+	+	+	+
—	1901	—	+	+	—	—	+
+	1903	—	+	+	—	—	+
—	1911	+	+	+	+	+	+
—	1914	—	+	+	—	—	+
+	1916	+	+	+	—	+	+
—	1918	+	—	+	+	+	+
—	1920	—	+	+	—	—	+
+	1922	+	—	+	+	+	—
—	1923	+	—	+	+	+	+
		16-11	15-12	17-10	13-14	16-11	17-10

with the lag effects somewhat more pronounced. Of the 27 critical years covered by the records at Lakeport, only 1894 did not show a corresponding supply of water, either through rainfall of the growing season or supplied by the ground as the result of relative drought or excessive rainfall during the snowless period of the preceding year. The latter seems to be much more important than water from the melting of the snowfall in winter which has been checked against growth rates (both alone and along with precipitation of other periods) and found to show no consistent relationships at either Hanover or Wakefield.

Similar studies for the other four sites could not be made for lack of suitable records of precipitation near the sites. The Wolfeboro site may or may not receive a rainfall like that of Wakefield but at least the like response of the growth processes is shown in figure 3 and table I. The Benton and Fairlee trees grew at some distance from any station with a weather record of adequate length. The lack of suitable data for the Windsor area has already been pointed out (Lyon, '35).

The general conclusion from these growth rate studies and analysis with reference to climatic factors is that the years indicated as either unfavorable or favorable for hemlock growth (table I), also mean years with corresponding droughts or well watered periods, of either the same spring and summer or the preceding snowless period or both, with the probabilities in favor of the same calendar year. To state the matter from the standpoint of tree growth, the soil must get (or lack) its moisture either from the supply left in the ground or from the rainfall of its growing season. The critical years thus detected are years with actual physiological drought or dampness.

From the standpoint of vegetation and crops, these years are more important than the years in which the water did or did not fall in its usual amounts or at its usual intervals. Furthermore, there is here no question of excessive run-off quantities as during heavy rains, or unusual interception of rainfall by foliage, as occurs during periods with frequent, light showers. These and certain other recognized factors make the ordinary weather records of limited value to ecology while physiological indices or indications are dependable, in so far as they are used with reference to the conditions under which they were derived. On the basis of these considerations and the evidence here presented, it seems possible to regard hemlock tree growth as a good index of physiological dryness in the area concerned.

It is possible to test this point further by comparing the critical years listed in table I with other records of notably poor or good seasons for plant growth. Such records are to be found in personal diaries and town or state histories which frequently refer to years of famine or of plenty as the result of crop failure or success because of climatic conditions.

A search for such records in northern New England has produced a few items from the approximate area covered by this study and the agreement is excellent. Farmer (unpublished diaries kept in southern New Hampshire)

noted dry growing seasons in 1821 and 1826 and the tree rings are narrow for those years. In Lynn, Mass., which is farther south, there are records of decided droughts for the years 1644, 1705, 1749, 1762 and 1854 (Lewis and Newhall, 1865). Only the first of these five years did not give narrow rings in the hemlocks but its drought affected New Hampshire trees one year later. Belknap's "History of New Hampshire" (1812) mentioned the droughts early in 1761 and 1762 and the narrow rings of 1780 at most of our sites also agree with Belknap's record that the winter of 1779-1780 was so "remarkably dry, without rain or thaw" that "springs of water were very low." Further evidence for a severe drought in 1780 is found in the famous dark day of May 19, 1780. According to Belknap (p. 22), it was due to the smoke pall from extensive forest fires in New England north of Dover, N. H.

The most valuable series of such observations was discovered for the area about Portland, Maine. This city lies at about the same latitude as our hemlock sites but its rainfall conditions are far from identical (Brooks, Weber and Richards, '30) for several reasons. In spite of these climatic differences, a long diary record of droughts at Portland support our tree ring records remarkably well. References to unusually good seasons for crops are less numerous in such personal records and so many variables and personal factors are involved that they are less dependable for comparison with uncultivated plants. This Portland record was kept by Rev. Thomas Smith (Willis, 1849) from 1726 until his death in 1787. The years in which he noted decided droughts of more than a few weeks duration have been entered in table IV which also shows in parallel all the drought years for hemlock growth in the area about a hundred miles to the west. Except for the two years 1727 and 1746, the latter with an admittedly late drought, the correlation is practically perfect: the hemlock trees record extended droughts of their area with a high degree of accuracy.

Smith's references to very good crops and rainy seasons numbered about 12 but only half of them coincided with unusual growth in hemlock although good correlations for such maxima were demonstrated above. A careful analysis of differences in the rainfall between Portland and New Hampshire would probably furnish the explanation for this discrepancy.

Aside from an explanation of why the graphs of ring widths should fluctuate up and down in essentially the same years, the resulting possibilities for cross-identification between trees should be noted briefly. It would be safer to use mean values of 2 or 3 good radii for any problem to which the method was applied, although a great many hemlock trees have the pattern or sequence of ring-widths represented fairly accurately in some one average radius. If a woodland area has an appreciable slope and other features which make for a small reserve of soil moisture, its trees can best be compared with those of a similar area; otherwise it may be necessary to allow for a variation of one year at various points along the time scale. A ring count of less than 50 will hardly permit accurate comparisons but 100 rings in an undated wood

TABLE IV. *Records from diaries of drought years and their correlations with narrow tree growth rings*

Records and comments	Narrow tree growth rings
1727 Hay scarce "on account of drought"	—
1736 Corn scarce following winter and summer	1735 } At Fairlee, 1736 } Hanover and 1737 } Wolfeboro only
1737 Dry May and autumn months	
1741 Hot and dry all summer	1741
1743 Dry April and June: streams low; hay scarce	1743
1746 Dry July and August only	—
1748 Severe drought following a dry fall and deep snow in winter	1748
1749 Dry until July 25th	1749
1754 Very severe drought	1754
1755 Warm, showery summer	1755
1761 Irregular drought until Aug. 15th	1761 } At Wolfeboro only
1762 Forest fires; public prayers and fast on account of the "grievous drought"	1762
1767 Warm and rain only in showers until August	1767
1768 Late spring; "A happy season for Indian corn"	1768
1770 Hot, rather dry summer	1770
1780 Dry May, June and July	1780

section will usually give a sequence of widths that can be recognized and dated. Some preliminary work now being done with white pine indicates that it too may be used for cross-identification purposes but only for comparisons between pine trees as hemlock must be used against hemlock.

Since this study of hemlock rings has produced evidence of good cross-identification as far back as the 16th century, it is also possible to obtain from their records some new information concerning the critical years for plant growth, especially during the 17th and 18th centuries. The years with particularly good or poor moisture conditions can be found in table I. It is possible that they alone will be of some aid in economic or historical studies of those centuries. The data for growth rates cannot be used in their present form as a definite measure of comparative growth conditions throughout the period covered but we hope to make some such use of them later, after applying the necessary corrections for growth rates at different ages and under different environmental conditions, other than those included by climate.

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SUMMARY

The annual rings of old hemlock trees (average age 279 years) have been carefully measured and graphs made from the mean values in order to show the fluctuations in radial growth rates from year to year. Cross-identification of individual trees within a forest and of groups of trees from several sites in Vermont and New Hampshire is entirely possible, due to dominance of the factor of physiological dryness within the area. Many years since 1600 are found to have been outstanding for the good moisture conditions available for plant growth. During the same three and a third centuries, about twice as many years are marked by actual physiological drought which retarded plant growth throughout the entire area. Cyclic effects are not evident. In general, the standard weather records of an area fail to indicate the years with particularly favorable or unfavorable conditions for growth while the hemlock tree, as used in this analysis, offers a better as well as much longer record of these conditions in its general locality.

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THE IDENTIFICATION OF GRASSES ON THE UPPER SNAKE RIVER PLAINS BY THEIR VEGETATIVE CHARACTERS

JOS. F. PECHANEC

Intermountain Forest and Range Experiment Station, Ogden, Utah

Grasses must be identified by their vegetative characters in early spring prior to flowering or at any time when flowerstalks are not available. Existing keys which stress flower and seed characteristics are of limited service to range investigators during these periods. It is the purpose of this paper, therefore, to present a usable key to some important range grasses of the West based entirely on vegetative characters.

The field data necessary for the construction of the key were obtained by studying important grass species occurring on or near to land leased by the Wool Growers of Fremont County, Idaho, located in and representative of, the upper Snake River plains. In this semi-arid area, native grasses are the principal forage species. Ranges of this character are used chiefly for spring-fall grazing.

The reliability and accuracy of the key and descriptions as presented herein were checked thoroughly by several members of the Intermountain Forest and Range Experiment Station during 1933 and 1934. The key proved accurate, practical to apply and useful, particularly during the unusually dry season of 1934 when few or no flowerheads were produced. Neither the key nor the descriptions have been fully checked on other range areas, but they are thought to be applicable to the upper Snake River plains, and in general to a wider territory.

PREVIOUS INVESTIGATIONS

The supply of literature is meager concerning identification of grasses by vegetative characters. Nothing of this character has been published on range grasses of the western United States. Studies by Stebler and Schröter ('89), McAlpine ('90), Ward ('01), Lewton-Brain ('04), Percival ('00), Carrier ('17), Beadle ('27), Ball ('27), Norton ('30), Whyte ('30), Copple and Aldous ('32), and Keim, Beadle and Frolik ('32) all dealing with flora unlike that presented herein, have afforded suggestions used in the construction of the key. The works of Carrier and of Keim, Beadle and Frolik were found to be helpful due to their thorough and well-illustrated discussion of the vegetative organs of grasses.

METHOD OF STUDY

Descriptions of each species of grass were recorded in the field, repeating frequently in order to secure characteristics at several stages of development

from start of growth until the herbage was cured. These descriptions of vegetative characters were checked with such descriptions as exist in standard botanical keys. When differences were found, field observations were rechecked to ascertain whether the discrepancies were due to inaccurate observation or to the influence of site.

VEGETATIVE CHARACTERS OF GRASSES

True grasses, with which this paper is concerned, include only those plants belonging to the family Gramineae or Poaceae. These can be distinguished from "grasslike plants" by the following characters: stems are jointed and usually hollow (except at the nodes); leaves are two ranked on opposite sides of the stem and composed of two parts—the blade, usually long and narrow with parallel venation and the sheath, tubular and enclosing the stem, with margins usually free; a ligule, usually occurring at the junction of the blade and sheath, is seldom wanting or reduced to hairs. Grasslike plants with which grasses may easily be confused belong to two groups: sedges, family Cyperaceae, characterized by three-angled, solid stems with leaves in three ranks; and rushes, family Juncaceae, characterized by solid unjointed stems, tube-like closed sheaths, cylindrical or straplike leaves neither folded nor rolled in the bud and without a ligule. Grasses may be annuals, or perennials. Perennials assume two definite forms: (1) tufted bunchgrasses, which reproduce almost entirely by seed; and (2) sod grasses, which, in addition to seed, reproduce vegetatively by means of rootstocks or of stolons.

Roots in all grasses are fibrous, and are not therefore important as a distinctive vegetative character.

Stems are of three kinds: (1) erect; (2) prostrate, rooting at the nodes and producing leaves (stolons) (fig. 3); and (3) prostrate underground, jointed stems having scalelike, reduced leaf sheaths (rootstocks) (fig. 4).

The *node* seldom is of any taxonomic importance, though in a few species it is bent sharply, and in some grasses is densely pubescent. The node commonly differs slightly in color from the sheaths and internodes.

Mode of arrangement of the leaf or leaves in the bud (vernation) is a very useful character, but one difficult to determine with involute or filiform leaves, which are here designated as *folded* (fig. 6). Leaves in general may be classified as *rolled* (fig. 5) or *folded*. Leaves rolled in the bud are generally associated with a round leaf shoot (fig. 1, *E*) and those folded in the bud with a flattened or terete leaf shoot. Some exceptions have a leaf folded in the bud but with a round leaf shoot.

A *grass leaf* is composed of two parts, the sheath and the blade.

The *sheath* (fig. 1, *D*) of grasses is characteristically *open* or split, that is, it surrounds the internode in such a manner that one margin overlaps the other from which it cannot be separated without tearing the sheath. Sometimes, however, the two margins may be united or *closed* nearly to the top of the

sheath. The margins may be thin, transparent and paperlike, or herbaceous and of the same texture as the sheath, or in some species ciliate or fringed with long hairs. The sheath may be round or flattened in cross section. *Venation* of the sheath is usually inconspicuous but in some species may appear as ridged or striated. The midrib of the blade may continue a short distance below the collar forming a keel at the back of the sheath.

Sometimes the sheaths, especially those near or at the ground surface, bear a tinge of red or purple color, which may be evenly distributed throughout or be concentrated in the veins. Such coloring in many cases disappears as the herbage nears maturity or as the season progresses. Other characters useful in the description of the sheath are: (1) presence or absence, and the degree of pubescence; (2) smooth or scabrous surface; (3) glaucous or green color, and (4) sheaths that are snug or loose on the internode.

The *blade* (fig. 1, *A*) may be flat, folded, involute, filiform, or keeled (fig. 14). The texture of the blade is classified, (*a*) as thin and papery, (*b*) as coarse and more or less leathery (coriaceous), or (*c*) as spongy. If the leaf tip is closed and shaped like the prow of a boat it is termed "boat-shaped," or it may be acute (fig. 12), or even acuminate and in some species it is prolonged into a long, sharp, callous tip (setaceous). The base tapers into the sheath (fig. 13), slightly, abruptly or with a definite curve. In some species the veins of the blade are so heavily covered with tissue on the upper side and the interspaces are so thin that the veins show readily by transmitted light as heavy, dark green, parallel striae. In other species the veins and interspaces are covered about evenly with tissue, the veins appearing only as fine indistinct lines scarcely discernible from the intervening tissue. In most species of *Poa* the tissue on either side is thin in comparison with the midrib. By transmitted light the midrib appears as if bordered by a fine white line (median line) on either side, the remainder of the blade being inconspicuously nerved and unridged. In some species the veins are so heavily covered that they stand out as parallel ridges, or striations, and the blade is said to be "striately nerved." These ridges may be sharp or flat-topped; prominent, medium, or inconspicuous. In a few species the veins may form ridges on the lower surface and in rare instances on both surfaces. The midrib may be covered with so much tissue on the lower side as to form a keel on the blade. Other characters often used in describing the blade are the presence or absence of pubescence, scabrous or smooth surface, and glaucous or green color. At the junction of the sheath and blade are three characters important in vegetative identification: (1) the auricles, (2) the collar, and (3) the ligule (fig. 2).

Auricles (fig. 2, *E*) are earlike appendages at the summit of the sheath, common in the tribe *Hordeae*. These appendages may be (*a*) short, obtuse, and upright; (*b*) short, acute, and horizontal but not clasping the stem; or (*c*) long, acute, and clasping (fig. 8). In most grasses the auricles are colorless or light green, but in a few species they are tinged with red or purple. Auricles are most distinct on fresh, young specimens more than 6 inches in

height. Only long, acute, and more or less clasping auricles are regarded as having classification value.

The *collar* (fig. 2, *C* and fig. 7) is a shelf-like, thickened, apparently veinless band marking the junction of the blade and sheath. Ordinarily it is

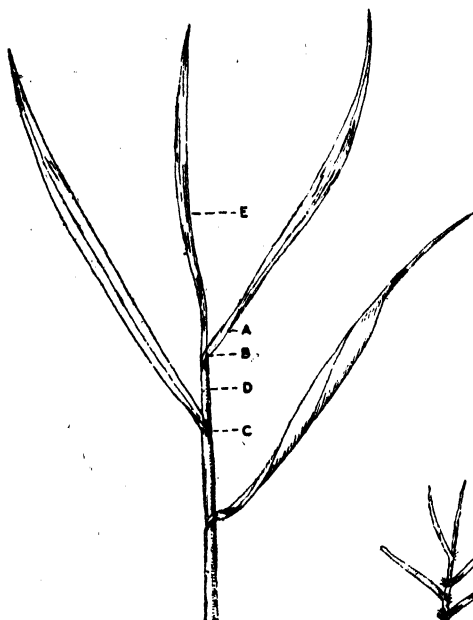


FIG. 1

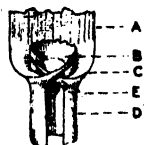


FIG. 2



FIG. 3

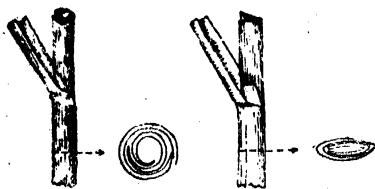


FIG. 5

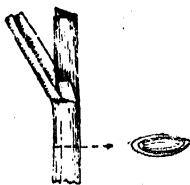


FIG. 6

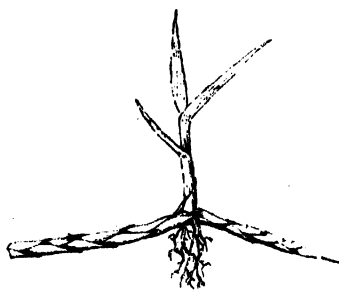


FIG. 4

FIG. 1. Vegetative parts of a grass: *A*, blade; *B*, ligule; *C*, collar; *D*, sheath; *E*, shoot or leaf bud.

FIG. 2. Parts at junction of blade and sheath: *A*, blade; *B*, ligule; *C*, collar; *D*, sheath; *E*, auricles.

FIG. 3. Reproduction by stolons.

FIG. 4. Reproduction by rootstocks.

FIG. 5. Arrangement of leaves in bud—rolled.

FIG. 6. Arrangement of leaves in bud—folded.

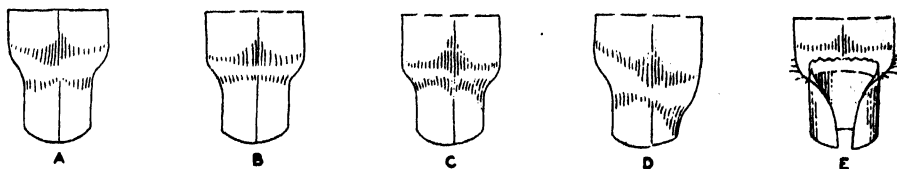


FIG. 7

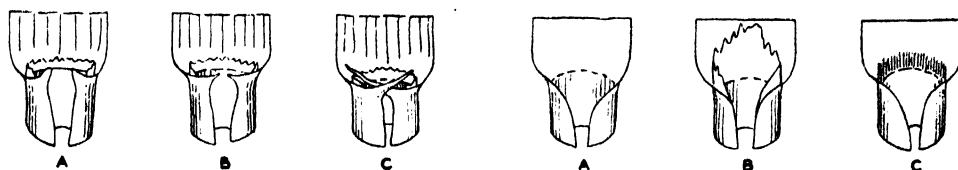


FIG. 8

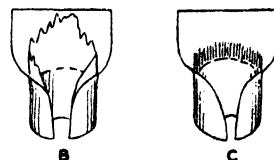


FIG. 9

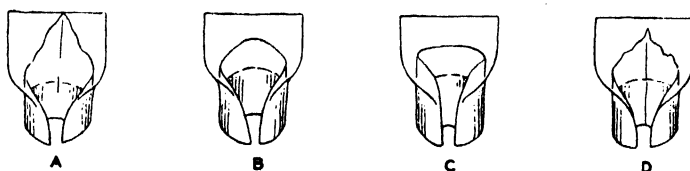


FIG. 10

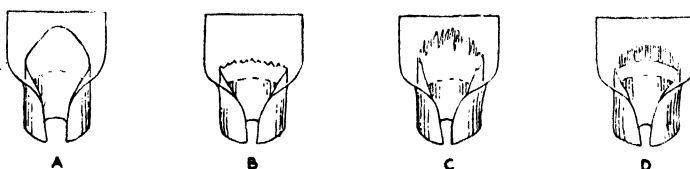


FIG. 11

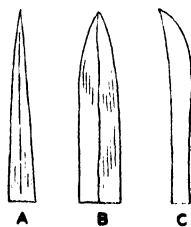


FIG. 12

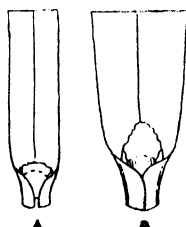


FIG. 13

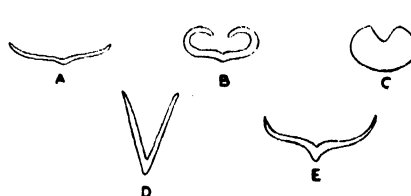


FIG. 14

FIG. 7. Collar types: *A*, broad; *B*, narrow; *C*, divided; *D*, spiral; *E*, hairy.

FIG. 8. Types of auricles: *A*, short, obtuse and upright; *B*, short, acute and horizontal; *C*, long, acute and clasping.

FIG. 9. Types of ligules: *A*, wanting; *B*, membranous; *C*, composed of hairs.

FIG. 10. Shape of ligules: *A*, acute; *B*, obtuse; *C*, truncate; *D*, mucronate.

FIG. 11. Margin of ligule: *A*, entire; *B*, crenate; *C*, lacerate; *D*, hairy margined.

FIG. 12. Tip of leaf: *A*, acute; *B*, boat-shaped; *C*, side view of boat-shaped.

FIG. 13. Base of leaf: *A*, little constricted; *B*, much constricted.

FIG. 14. Leaf blade types: *A*, flat; *B*, involute; *C*, filiform; *D*, folded; *E*, keeled.

slightly lighter in color than the rest of the leaf, though in some species it may be tinged with red or purple. In most grasses the collar is continuous from one margin of the sheath or blade to the other, but in some species it is divided by the midnerve (fig. 7, C). Occasionally the collar is pubescent on the back or front and sometimes ciliate on the margin with long pilose hairs (fig. 7, E). It may be broad and conspicuous, or narrow and indistinct (fig. 7).

The *ligule* (fig. 2, B) with all of its many variations is probably a continuation of the lining of the sheath, and with the collar has been credited with the function of preventing rain and dew from running down inside the sheath and encouraging rot. The ligule, usually a hyaline membrane, is in some grasses wholly absent or composed entirely of hairs (fig. 9). Because of its several stable forms, the ligule is one of the most dependable characters for identification. In the use of the key a ligule that is less than 2 mm in length is classified as short, more than 2 mm, as long. A ligule may have a tip that is acute, obtuse, or truncate (fig. 10); a margin that is entire, toothed, or hairy, (fig. 11); a back that is glabrous or pubescent, especially near the base.

CONSTRUCTION OF THE KEY

Only the most reliable and constant characters are used in this key. In construction, the contrasting characters are in pairs under which the various species are grouped. The number affixed to the species name indicates the order of the species in the formal descriptions. To become acquainted with the key and with the terms used, one should follow specimens of known grasses through the key. Formal descriptions of species are included with which to check the identification.

It should be noted that certain species do not immediately assume all of their vegetative characters. This is especially true in several members of the genera *Elymus*, *Agropyron* and *Hordeum*, in which the auricles do not ordinarily appear until the plants have attained a height of 4 to 6 inches. Two safe guides are to exclude all seedling and perennial specimens that have not developed at least a second, or still better, a third leaf, and to base identification only on several specimens.

Degree of pubescence and exact size are not included in the descriptions, since both characters vary with site, for which reason they are measured only in relative terms and used merely as identification aids. One means of observing the degree of venation, the depth of ridges along with the shape of the top of the ridges and the degree of pubescence on either blade surface, is to roll the blade over the finger and look along the veins against the lighter background.

To determine whether the blade is folded or rolled in the shoot, a cross-section of the shoot is cut immediately below the throat of the sheath and examined with a lens. The cross-section can be brought out more distinctly by allowing a short period for bleeding. An alternative method is to strip

a leaf from the young shoot and examine it with a lens. With a little practice and careful observation it is not difficult to see whether the leaf is rolled or folded in the shoot. Grasses having tightly involute or filiform blades are usually folded in the bud.

VEGETATIVE KEY TO GRASSES OF THE SNAKE RIVER PLAINS

- A. Tip of blade boat-shaped; leaves folded in bud; median lines present, pubescence very short or none, blade inconspicuously nerved, sheath flattened or round...*Poa*
- B. Tufted perennials; rhizomes absent; sheaths round or slightly flattened.
 - C. Ligule 2-6 mm long; leaves 5-25 cm long, 2-4 mm wide, leaves moderately to harshly scabrous1. *Poa nevadensis*
 - CC. Ligule 1-3 mm long; leaves 2.5-10 cm long, usually less than 2 mm wide, leaves smooth to moderately scabrous2. *Poa secunda*
- BB. Rhizomes present; sheath conspicuously flattened3. *Poa pratensis*
- AA. Tip of blade acute or abruptly tipped, not boat-shaped, median lines absent.
 - B. Auricles usually present, clasping; leaf rolled in bud; sheath round; leaf striately nerved above.
 - C. Blade broad, 6-24 mm wide; ligule 2-5 mm long, obtuse; rhizomes usually absent4. *Elymus condensatus*
 - CC. Blade narrow, usually less than 6 mm wide; ligule short, less than 1 mm long, truncate.
 - D. Blade and sheath conspicuously pubescent above and below, with soft short hairs; blade soft and lax, smooth or slightly scabrous5. *Sitanion hystrix*
 - DD. Blade glabrous below, scabrous at least above, not soft.
 - E. Rhizomes present; blade often more than 3 mm wide, sparsely strigose pubescent or glabrous above...6. *Agropyron dasystachyum*
 - EE. Rhizomes absent.
 - F. Blade usually less than 3 mm wide, densely strigose pubescent above, auricles and collar usually somewhat reddish tinged; sheath never pubescent7. *Agropyron spicatum*
 - FF. Blade often more than 3 mm wide, glabrous or only slightly strigose pubescent above; auricles and collar rarely reddish tinged; sheath sometimes pubescent ..8. *Agropyron cristatum*
 - BB. Auricles absent.
 - C. Ligule usually composed of hairs; collar pubescent with long hairs; leaves rolled in bud9. *Sporobolus cryptandrus*
 - CC. Ligule membranous; collar glabrous or pubescent with short hairs.
 - D. Blade pubescent above and below; sheath pubescent; blade flat or drying involute, never involute-filiform; leaf rolled in bud.
 - E. Ligule truncate, less than 0.5 mm long; sheath open; auricles sometimes present; perennial5. *Sitanion hystrix*
 - EE. Ligule obtuse, usually longer than 0.5 mm; sheath closed nearly to summit; auricles absent; slender annual...10. *Bromus tectorum*
 - DD. Blade at least glabrous below or if pubescent involute-filiform; sheath usually glabrous; leaf rolled or folded in bud.
 - E. Ligule usually less than 2 mm long, truncate or obtuse.
 - F. Ligule 0.5-2 mm long; blade flat, prominently striately nerved.
 - G. Rhizomes present; ligule 1-2 mm long; blade acutely tipped11. *Muhlenbergia squarrosa*
 - GG. Rhizomes absent; ligule 0.5-1 mm long; blade abruptly tipped12. *Koeleria cristata*

- FF. Ligule 0.1–0.5 mm long; blade flat to involute filiform, slightly to moderately striately nerved, acutely tipped.
- G. Blade involute filiform, usually less than 1 mm wide; sheath glabrous; blade canescent above, glabrous below
13. *Oryzopsis webberi*
- GG. Blade flat or drying involute, yellowish-green to green, glabrous or sparsely pubescent.
- H. Sheath purplish below and above ground; blade 2–5 mm wide, 10–50 cm long; ligule entire or toothed; plant loosely tufted ..14. *Stipa columbiana nelsonii*
- HH. Sheath white below and above ground; blade 1–3 mm wide, 10–30 cm long; ligule ciliate; plant densely tufted15. *Stipa columbiana*
- EE. Ligule 2–8 mm long, obtuse or acute; blade acutely tipped.
- F. Rhizomes present; leaf rolled in bud; ligule acute, glabrous; blade scabrous above and below
16. *Calamagrostis montanensis*
- FF. Rhizomes absent; leaf folded in bud; ligule obtuse or mucronate.
- G. Ligule sparsely pubescent or glabrous; collar pubescent on margin with a few short hairs; blade usually tightly involute, smooth and shiny below
17. *Oryzopsis hymenoides*
- GG. Ligule densely pubescent on back, notched or split in back; collar glabrous; blade flat or involute, slightly scabrous below, not shiny18. *Stipa comata*

DETAILED VEGETATIVE DESCRIPTION OF GRASSES

1. *Poa nevadensis* Vasey (Nevada bluegrass).

Low, tufted glabrous perennial; shoot flattened to round, leaf folded in bud; sheath round to scarcely flattened, open, glabrous (pubescence sometimes present, visible only with lens), margins hyaline, continuous with ligule, white to purple below ground, veins indistinct, harshly scabrous; ligule 1–6 mm long, membranous, acute, toothed, glabrous or scabrous on back; collar medium to narrow, indistinct, yellowish-green, continuous, glabrous; auricles absent; leaf blade 2–4 mm wide, 5–25 cm long, flat to V-shaped, not constricted at base, gradually tapering, tip boat-shaped, veins indistinct, median lines present, margins smooth to scabrous, very harshly scabrous, glabrous, dark green.

2. *Poa secunda*, Presl. (Sandberg bluegrass).

Low, tufted perennial with cushion of leafy blades at the base; leaf folded in bud; sheath round to scarcely flattened, open, glabrous, margins hyaline, white to reddish below ground; veins indistinct, smooth or slightly scabrous; ligule 1–3 mm long, entire, acute; collar narrow, indistinct, continuous or divided, glabrous; auricles absent; leaf blade 1–2 mm wide, 3–7 cm long, flat to V-shaped, not constricted at the base, gradually tapering, tip boat-shaped, veins indistinct, median lines present, margins smooth to scabrous, glabrous, yellowish-green to green.

3. *Poa pratensis* L. (Kentucky bluegrass).

Low, glabrous perennial spreading by rootstocks; shoot flattened; leaf folded in bud; sheath flattened open, glabrous, smooth or slightly scabrous, colorless; ligule 1–3 mm long, short, acute or obtuse, entire, glabrous; collar medium to narrow, continuous or

divided by midrib, glabrous; auricles absent; leaf blade 1-3 mm wide, 5-15 cm long, flat to V-shaped not constricted at the base, tip boat-shaped, veins indistinct, median lines present, smooth to scabrous, glabrous or very slightly pubescent above, green.

4. *Elymus condensatus* Presl. (Giant wild-rye).

Large, glaucous, glabrous, tufted perennial; shoot round, leaf rolled in bud; leaf sheath round, red or purplish at and below ground in spring, glabrous, veins distinct, open, margins hyaline; ligule long, 2-5 mm, obtuse, coarsely toothed, glabrous; collar broad, distinct, yellowish-green, continuous, glabrous; usually spiral; auricles large, obtuse or acute, clasping, glabrous; leaf blade broad (6-24 mm), 15-50 cm long, flat, somewhat constricted at the base, gradually tapering, tip more or less abruptly pointed, somewhat twisted, prominently striately nerved above and slightly below, margins moderately barbed, scabrous above smooth below, glabrous, yellowish-green to dark bluish-green, erect.

5. *Sitanion hystrix* (Nutt.) J. G. Smith (Squirreltail)

Slender, erect, leafy perennial clothed at base with papery leaf sheaths; shoot round, leaf rolled in bud; leaf sheath round or slightly flattened, purple below ground, open, margins hyaline, pubescent (hairs soft, short 0.2-0.5 mm long), ligule short (0.5 mm long), erose truncate; collar medium to broad, whitish-green or tinged with red, pubescent, not spiral; auricles present or absent, short, acute, clasping, tinged with red; leaf blade narrow, 2-3 mm wide, 7-12 cm long, flat or drying involute, slightly constricted at base, gradually tapering to tip, slightly twisted, striately nerved above, 8-9 nerved, midvein not prominent below, smooth or slightly scabrous, softly and minutely pubescent above and below, soft and lax, bluish-green.

6. *Agropyron dasystachyum* (Hook.) Scribn. (Thickspike wheatgrass)

Slender, glaucous perennial from rootstocks; shoot round, leaf rolled in bud; leaf sheath round, white to pinkish below ground and immediately above, glabrous, smooth, veins distinct, usually open at least halfway; ligule very short, truncate, erose; collar narrow to medium, distinct, continuous, often tinged with red in the spring, glabrous or pubescent; auricles long, acute, tinged with red in spring, glabrous or pubescent; leaf blade 1-4 mm wide, 5-25 cm long, flat, drying involute, little constricted at the base, midvein not distinct on lower surface, slightly twisted, striately veined above, scabrous above, smooth below, sparsely strigose or glabrous above, yellowish-green to dark green, erect, stiff.

7. *Agropyron spicatum* (Pursh) Scribn. & Smith (Bluebunch wheatgrass)

Slender, rather wiry, densely tufted perennial; shoot round, leaf rolled in bud; leaf sheath round, red to purple below ground, glabrous, slender, veins indistinct, open, margins hyaline, smooth; ligule very short (.5 mm), truncate, erose, glabrous; collar narrow, tinged with purple or red in spring and often later, glabrous, divided or continuous; auricles long, clasping, twisted, tinged with red or purple, glabrous; leaf blade 1-3 mm wide, 5-15 cm long, flat or drying involute, little constricted at base, tapering to tip, little twisted, prominently striately nerved, midvein not prominent below, margins scabrous, scabrous above, smooth below, densely strigose pubescent above, glabrous below, yellowish-green to bluish-green, erect, dried herbage conspicuously curled and twisted.

8. *Agropyron cristatum* (L.) Gaertn. (Crested wheatgrass)

Densely tufted, green perennial; shoot round, leaf rolled in bud; leaf sheath round, pinkish to purplish below ground, glabrous, sometimes pubescent with soft spreading hairs, veins distinct, open (sometimes lower sheaths closed), slightly scabrous; ligule

very short, erose truncate, ciliate; collar narrow to medium, distinct, glabrous or pubescent; auricles usually present, long, acute, glabrous or pubescent; leaf blade long 2-7 mm wide, flat, somewhat constricted at the base, tapering to tip, usually twisted, striately nerved above, midnerve prominent at base below, margin scabrous, scabrous above and somewhat below, blade glabrous or very slightly strigose above, lax and spreading, dark green, dull.

9. *Sporobolus cryptandrus* (Torr.) A. Gray (Sand dropseed).

Smooth, semidecumbent perennial, often densely caespitose and with numerous short basal leaves; shoot round, leaf rolled in bud; leaf sheath round or slightly flattened, glabrous except for long, appressed, sometimes spreading hairs on the hyaline margin; open, crowded at base; ligule short, truncate, hairy margined or composed entirely of hairs; collar broad, continuous, glabrous except for tuft of long villous hairs each side of throat; auricles absent; leaf blade flat, short, medium in width; tip acuminate, spreading and somewhat drooping, striately nerved above, scabrous above and on margins.

10. *Bromus tectorum* (L.) (Downy bromegrass).

Pale green, pubescent, simple or tufted annual; shoot round, leaf rolled in bud; leaf sheaths round or slightly flattened, pubescent with a short silky pubescence, closed, keeled nearly to the summit with a continuation of the midnerve; ligule short, truncate or obtuse, toothed, glabrous; collar narrow, continuous, pubescent, tinged with purple; auricles none; leaf blades flat, 2.5-10 cm long, 2-4 mm wide, tips acute, somewhat keeled especially at base, pubescent with short, silky pubescence; veins of lower sheaths in early spring pink.

11. *Muhlenbergia squarrosa* (Trin.) Rydb. (Mat muhly).

Low, glabrous, wiry perennial, tufted or from short scaly rootstocks, stems decumbent at the base; shoot slightly flattened to round, leaf rolled in bud; sheath slightly flattened to round, open, margins hyaline, continuous with ligule, glabrous, smooth to slightly scabrous, veins distinct; ligule 1-2 mm long, obtuse, back slightly to conspicuously pubescent; collar narrow to medium, continuous, glabrous; auricles absent; leaf blade narrow, 1-2 mm, 2-10 cm long, flat or drying involute, glabrous, striately nerved above, slightly to harshly scabrous, slightly constricted at the base, tapering to the tip, glabrous below, acute tipped, erect, grayish-green.

12. *Koeleria cristata* (L.) Pers. (Junegrass)

Erect, perennial grass with numerous basal leaves; shoot round, leaf folded in bud; leaf sheath round or slightly flattened below ground, glabrous or pubescent with very fine, short retrorse hairs, veins distinct, open margins hyaline; ligule very short, .5 mm long, truncate or obtuse, erose, sometimes split, ciliate; collar narrow to medium, continuous or divided yellowish-green, glabrous or pubescent; auricles absent; leaf blade 1-3 mm wide, 5-25 cm long, flat, slightly constricted at base, gradually tapering, tip bluntly pointed (nearly boat-shaped), slightly twisted, prominently striately nerved, midvein distinct below, margins barbed, upper surface scabrous, lower smooth, glabrous or pubescent, yellowish-green to glaucous.

13. *Oryzopsis webberi* (Thurb.) Benth. (Webbers mountain-rice).

Low, densely tufted, glabrous perennial; shoot slightly flattened, leaf folded in bud; sheath terete to flattened, open, glabrous, smooth to slightly scabrous, margins hyaline, veins distinct; sheaths crowded at base of plant and overlapping; ligule very short, obtuse or truncate; collar very narrow (a line), continuous, slightly raised or swollen, glabrous on back; auricles absent; leaf blade very narrow, 1 mm wide, 3-20 cm long, lightly

involute to filiform, tip acute, slightly to coarsely scabrous, canescent on upper inrolled surface, especially visible near collar, stiff, erect.

14. *Stipa columbiana* var. *nelsonii* (Scribn.) Hitchc.

Loosely tufted, glabrous perennial; shoot slender, round or slightly flattened, leaf rolled in bud; sheath slender, round purplish above and below ground, open, margins hyaline, ciliate, sheath often pubescent (very short); collar narrow, continuous, whitish glabrous or pubescent; ligule very short, 0.1 to 0.5 mm, truncate, entire or toothed; auricles none; leaf blade 2-5 mm wide, 10-50 cm long, flat or drying involute, somewhat constricted at the base, gradually tapering to the long setaceous tip, usually twisted, somewhat striately nerved above, more or less keeled on back with midnerve, sometimes ciliate on margins near throat, scabrous above and usually below, yellowish-green to green.

15. *Stipa columbiana* Macoun. (Columbia needlegrass).

Erect, densely tufted, glabrous perennial; shoot round, leaf folded in bud, leaf sheath slender, round to slightly flattened, white below, smooth, glabrous, margins hyaline and pubescent; collar narrow, indistinct, continuous, glabrous; auricles none; ligule 0.1 to 0.5 mm long, truncate, ciliate; leaf blade 1-3 mm wide, 10-30 cm long, flat or drying involute, slightly constricted at the base, gradually tapering to the acute tip, slightly twisted, somewhat striately nerved above, more or less keeled by midvein below, harshly scabrous above, smooth or slightly scabrous below, glabrous, thin in texture, yellowish-green, shiny, erect.

16. *Calamagrostis montanensis* Scribn. (Plains reedgrass)

Stoloniferous, erect, rigid perennial; shoot round, slender, leaf rolled in bud; leaf sheath slender, open, margins hyaline, glabrous, more or less scabrous, terete, lower sheath purplish below ground; collar narrow, continuous, glabrous, somewhat spiral, yellowish-green; ligule 2-5 mm long, usually acute, long pointed, toothed at and near apex, glabrous, continuous with hyaline margins of sheath; auricles absent; leaf blade flat, or soon involute, narrow (2-3 mm wide), 5-25 cm long, little constricted at base, gradually tapering to tip, slightly to harshly scabrous above and below, prominently striately nerved above, often strigose pubescent above, little twisted, grayish-green to bluish-green often marked on back with 1-3 darker lines, erect.

17. *Oryzopsis hymenoides* (Roem. & Schult.) Ricker (Indian ricegrass)

Dark green, glabrous, tufted perennial; shoot round or slightly flattened, leaf folded in shoot; leaf sheath round; slender, white to purplish below ground, glabrous, smooth, open, margins hyaline, veins indistinct; ligule 2-8 mm long, obtuse or acute, lacerate, glabrous or pubescent on back, continuous with hyaline margins of sheath; collar inconspicuous, pubescent on margin with a few short hairs; leaf blade 1-2 mm wide, 10-30 cm long, slender, involute (U-shaped to folded), thick, striately veined above, not constricted at base, gradually tapering to tip, little twisted, veins prominent, smooth below, scabrous above, often slightly pubescent on upper surface, dark green and shiny beneath, very long and slender, tightly involute.

18. *Stipa comata* Trin. & Rupr. (Needle-and-thread)

An erect, tufted perennial; shoot round to flattened, folded in bud; sheath slender, round to slightly flattened, open, margins hyaline, white to purplish below ground, glabrous or pubescent with short retrorse hairs, veins more or less distinct, scabrous; ligule 1-4 mm long, obtuse or truncate, occasionally more or less notched densely strigose pubescent on back; collar broad, continuous, glabrous or pubescent, whitish, not spiral;

auricles absent; leaf blade 1-2 mm wide, 5-25 cm long, flat, curling involute, not constricted at the base, gradually tapering, tip acute, more or less twisted, prominently striately nerved above, midvein indistinct, scabrous above and below, usually densely strigose above, sometimes below, green to bluish-green, erect.

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A WINTER BIRD COMMUNITY IN WESTERN NEW YORK

WILLIAM C. VAN DEVENTER

St. Viator College, Bourbonnais, Ill.

Although the tendency of birds of different species to associate in loosely-knit flocks in winter has been frequently noted, there has been no systematic analysis of such flocks and their component species from the standpoint of habitat preference and reaction to particular environmental factors. The present study involves an analysis of the activity of a four-species habitat group, consisting of the northern downy woodpecker, *Dryobates pubescens medianus* (Swainson), the northern white-breasted nuthatch, *Sitta carolinensis carolinensis* Latham, the black-capped chickadee, *Penthestes atricapillus atricapillus* (Linnaeus), and the eastern tree sparrow, *Spizella arborea arborea* (Wilson). This group was studied with reference to selection of community type, horizontal level of activity, response to temperature and general weather conditions, number of birds per unit of area, and percentage of association among members of the group.

The study was carried on during December, 1934, and January and February, 1935, in connection with a survey of the wild life of a game and nature preserve in Monroe County, New York, undertaken for the Monroe County Park Commission. The preserve, known as Mendon Ponds Park, comprises approximately 1700 acres. The land consists mostly of gravel hills, among which are numerous dry kettle holes, and several swamps and small lakes. Approximately half of the land was farmed before 1928, when the preserve was created. Very little reforestation has been done, and the abandoned fields are now weedy meadows with occasional scattered shrubs. Along the old field borders there are a few trees and a great deal of shrubby growth. Nine old dwelling sites with abandoned orchards are included in the area.

There are approximately 400 acres of forest in the preserve, including about 40 acres of swampy woodland. The beech, which occurred in the upland forest before the land was settled, has mostly been cut, and only young beech is now found. Otherwise the upland forest has been relatively unmolested.

The following community types occur in the preserve: (1) Open Lake, (2) Swamp, (3) Swamp Edge, (4) Swampy Woods, (5) Upland Woods, (6) Forest Edge, (7) Isolated Thicket, (8) Open Weedy Meadow, (9) Brushy Fence Row, (10) Abandoned Orchard, (11) Dwelling Environs.

The dominant and chief subdominant plants for each type are shown in the accompanying table (table I).

TABLE I. *Plants characteristic of community types*

Community Type	Dominants	Chief Subdominants
Open Lake	(Frozen in winter.)	
Swamp	<i>Vaccinium corymbosum</i> , high bush blueberry. <i>Potentilla fruticosa</i> , shrubby cinquefoil. <i>Chamaedaphne calyculata</i> , leatherleaf.	<i>Andromeda glaucophylla</i> , bog rosemary. <i>Vaccinium macrocarpum</i> , cranberry.
Swamp Edge	<i>Salix</i> sp., willow. <i>Populus</i> sp., aspen. <i>Larix laricina</i> , tamarack. <i>Alnus incana</i> , speckled alder.	<i>Cornus stolonifera</i> , red-osier dogwood. <i>Viburnum dentatum</i> , arrow-wood. <i>Vitis</i> sp., grape. <i>Rubus</i> sp., raspberry. <i>Solanum dulcamara</i> , night-shade.
Swampy Woods	<i>Acer rubrum</i> , red maple. <i>Ulmus americana</i> , elm. <i>Fraxinus</i> sp., ash.	<i>Sambucus canadensis</i> , common elder. <i>Solanum dulcamara</i> , night-shade. <i>Gaultheria procumbens</i> , winter-green.
Upland Woods	<i>Quercus alba</i> , white oak. <i>Acer saccharum</i> , sugar maple. <i>Quercus rubra</i> , red oak.	<i>Cornus florida</i> , flowering dogwood. <i>Hamamelis virginiana</i> , witch hazel. <i>Amelanchier canadensis</i> , shadbush. <i>Amelanchier spicata</i> , long-rooted shadbush.
Forest Edge	<i>Populus</i> sp., aspen. <i>Sassafras variifolium</i> , sassafras. <i>Prunus virginiana</i> , choke cherry. <i>Prunus pennsylvanica</i> , bird cherry. <i>Crataegus</i> sp., hawthorn.	<i>Hamamelis virginiana</i> , witch hazel. <i>Rhus typhina</i> , staghorn sumac. <i>Rubus</i> sp., raspberry. <i>Cornus stolonifera</i> , red-osier dogwood. <i>Vitis</i> sp., grape.
Isolated Thicket	<i>Rhus typhina</i> , staghorn sumac. <i>Sambucus canadensis</i> , common elder. <i>Cornus stolonifera</i> , red-osier dogwood. <i>Myrica carolinensis</i> , bayberry.	<i>Rosa humilis</i> , pasture rose. <i>Rubus</i> sp., raspberry. <i>Vitis</i> sp., grape.
Open Weedy Meadow	Miscellaneous grasses. Compositae	<i>Verbascum thapsus</i> , great mullein.
Brushy Fence Row	<i>Quercus alba</i> , white oak (occasional). <i>Prunus virginiana</i> , choke cherry. <i>Prunus pennsylvanica</i> , bird cherry. <i>Rhus typhina</i> , staghorn sumac. <i>Cornus stolonifera</i> , red-osier dogwood.	<i>Vitis</i> sp., grape. <i>Pseuderanthus quinquefolia</i> , Virginia creeper. Compositae. Miscellaneous grasses.

TABLE I. (Continued)

Community Type	Dominants	Chief Subdominants
Abandoned Orchard	Domestic apple. Domestic sweet cherry. Domestic pear.	<i>Cornus stolonifera</i> , red-osier dogwood. <i>Sambucus canadensis</i> , common elder. Compositae. Miscellaneous grasses.
Dwelling Environs	Various planted shade, fruit, and nut trees.	Ornamental shrubs. Domestic grape. Lawn grasses.

At least half of these community types were traversed in the course of each observational trip, and most trips included all of them. Each trip covered thoroughly an average area of 40 acres (one-sixteenth square mile). The study included a total of 36 trips, and 84 separate observations. Each observation consisted of seeing birds of one or more species at one time in a particular community type. In connection with each observation the following data were recorded: (1) Community type where found, (2) Horizontal levels involved in activity, (3) Species found in association, (4) Number of birds of each species in flock.

In addition the temperature and general weather conditions were noted in connection with each trip.

RELATION TO COMMUNITY TYPE

As a group the four species of birds showed a marked preference for the swamp edge. A lesser concentration of activity was noted in the dwelling environs and in the upland forest edge. The swamp and the open meadow were almost entirely unfrequented by these birds. Figure 1 shows the relations of the four-species habitat group to the community types arranged in a natural series from open lake to dwelling environs. In this graph the ordinates represent total numbers of observations for each species in each community type.

The white-breasted nuthatch was the most widely ranging species of the group. The observations for this species were almost equally divided between the swamp edge and the dwelling environs, and it also showed some tendency to be active in the upland woods. The downy woodpecker exhibited a stronger preference for the swamp edge, but showed a definite secondary preference for the dwelling environs. These two species were more likely to be observed singly or in pairs, and apparently were less closely tied to the habitat group than were the chickadee and the tree sparrow.

The two latter species apparently formed the nucleus of the group. They both exhibited a marked primary preference for the swamp edge, and only minor secondary preferences for the dwelling environs and the upland forest edge.

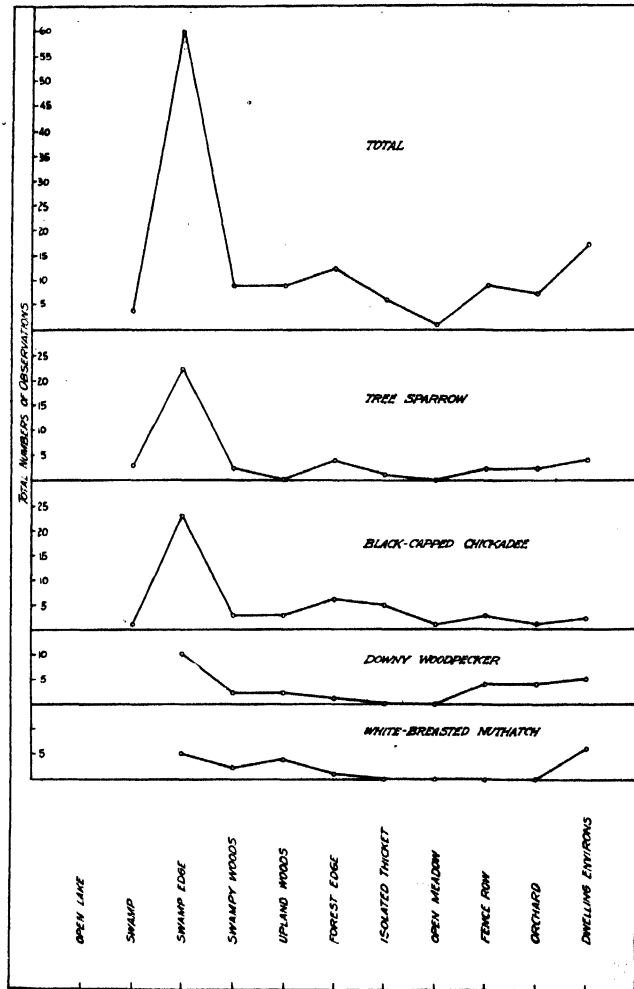


FIG. 1. Relation of the observed activity of the four-species habitat group of winter birds to community types. The modes indicate centers of activity for the group and its component species in particular community types.

RELATION TO HORIZONTAL LEVEL

Within all community types all four species showed a pronounced preference for the lower horizontal levels. Of the observed activity of the entire group, 81.3 per cent took place between the ground and the twenty-foot level.

The tree sparrow and the chickadee were the only members of the group which spent any appreciable amount of time on the ground. The nuthatch and the downy woodpecker were each observed on the ground on only two occasions. The tree sparrow, the chickadee, and the downy woodpecker were most active between the ground and the ten-foot level. This corresponds closely to the shrub layer of the community.

The nuthatch divided its major activity almost equally between the zone extending from the ground to ten feet, and the zone extending from ten to twenty feet. This latter zone was also occupied to some extent by each of the other species, but the downy woodpecker and the chickadee were relatively more active in it than the tree sparrow. This zone corresponds in general to the tall shrub and low tree layer of the community.

The relations of the activity of the group to horizontal level are summarized in figure 2. In this graph the ordinates represent the total numbers

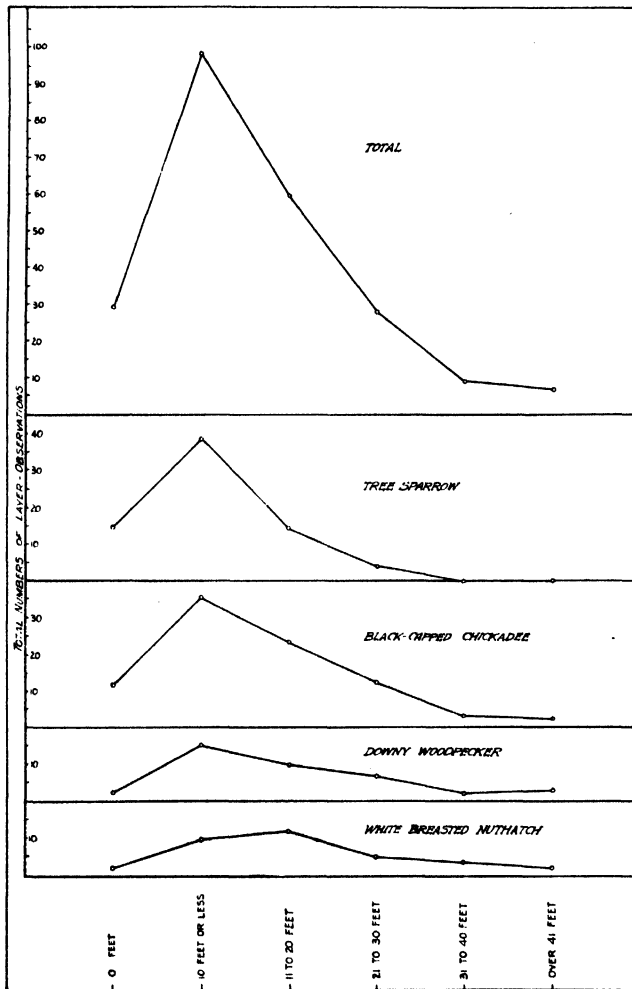


FIG. 2. Vertical distribution of the observed activity of the four-species habitat group of winter birds. The vertical region between the ground and a height of 40 feet is divided into horizontal zones at ten-foot intervals.

of layer-observations for each species. In determining these totals each observation for each species was multiplied by the number of horizontal zones in which that species was observed on that particular occasion.

RELATION TO GENERAL WEATHER CONDITIONS

There was no discoverable relation between the activity of the birds and temperature. However the activity of all four species exhibited a very marked relation to general weather conditions. The nuthatch, the tree sparrow, and the downy woodpecker showed the greatest amount of activity on partly cloudy days; while the chickadee was most active on sunshiny days.

All four species showed a marked depression in activity on completely cloudy days when there was no precipitation. In the case of each species, however, there was a slight but definite increase in activity on cloudy days when either rain or snow was falling.

In figure 3 the activity of the birds is plotted in relation to weather conditions. In order to represent this activity graphically, the presence of a species in any one horizontal zone on a particular occasion was considered as representing one "vertical activity unit." Thus the number of observed vertical activity units for any species on any single occasion corresponded to the number of horizontal zones which the species was seen to occupy during the period of observation. The total number of observed vertical activity units for a species on a particular type of day was divided by the number of observational trips taken on that type of day. The average number of observed vertical activity units per trip was thus secured. The ordinates of figure 3 represent these averages for each species on each type of day.

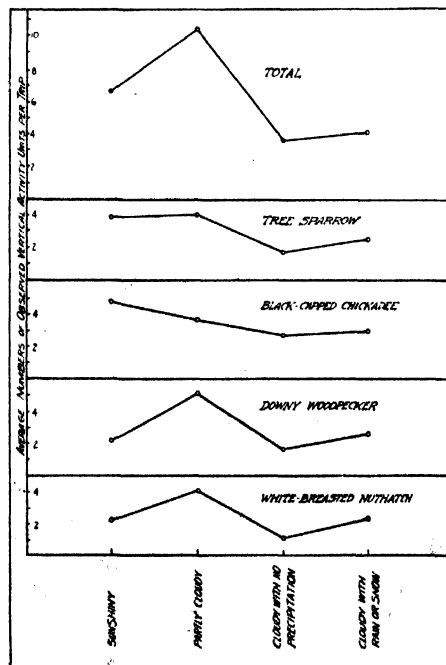


FIG. 3. Relation of the observed activity of the four-species habitat group of winter birds to gross weather conditions.

It will be noted from this graph that the nuthatch and the downy woodpecker were apparently more sensitive to gross weather changes than were either the chickadee or the tree sparrow.

NUMBER OF BIRDS PRESENT

From the number of birds of each species seen on an average trip, it was possible to estimate the approximate number which were present on a square mile. Each trip was estimated to cover thoroughly approximately 40 acres (one-sixteenth square mile). The following table (table II) shows the

TABLE II. *Estimates of Abundance*

Species	Ave. per Trip	Estimated Ave. per Sq. Mi.
Tree Sparrow	14	224
Black-capped Chickadee	8	128
Downy Woodpecker	2.33	37
White-breasted Nuthatch	2.12	34
Total	26.45	423

average for each species per trip, and the estimated abundance of each species on a square mile.

The four species comprising this habitat group include the great majority of winter birds, excepting gallinaceous birds, waterfowl, and predatory forms, which were present in the area in the open country. Therefore the total number of birds of these species present on a square mile may be compared with the estimates of bird density per square mile in winter in other regions having a similar climate.

Forbes ('23) obtained an estimate of 420 birds per square mile in northern Illinois, and 440 per square mile in central Illinois, in winter. These estimates correspond very closely to the estimate of 423 per square mile obtained for western New York in the present study.

Butts ('27) in studying the feeding habits of winter birds at Ithaca, New York, found that one pair of nuthatches normally ranged over about 48 acres, and that no other nuthatches were found in this area. This agrees very well with the average of 2.12 nuthatches per area of 40 acres found in the present study.

Bird ('29) in his study of the aspen forest of Manitoba found 40 chickadees and 12 downy woodpeckers per square mile in winter. In this case the ratio of the number of woodpeckers to the number of chickadees was approximately the same as that found in western New York, although the actual density of each species was only about one-third as great. This smaller population may probably be accounted for by the more rigorous winter climate of Manitoba.

FREQUENCY OF ASSOCIATION OF SPECIES

The frequency with which members of this habitat group are found together in winter has been noted by a number of observers. Eaton ('14) and Chapman ('34) mention the association in winter of the white-breasted nuthatch, the downy woodpecker, and the black-capped chickadee. Butts ('27) mentions the association of these three species, and records the tree sparrow from the same general area. He says: "Perhaps one-sixth of the time when under observation nuthatches and chickadees were together." Bird ('29) lists the chickadee and the downy woodpecker as members of the same aspen forest winter community, and says that the chickadee inhabits the shrub layer in winter. With the exception of the statement quoted from Butts ('27) regarding the association of nuthatches and chickadees, however, the frequency of association of the species forming this habitat group is in no case numerically expressed.

In the present study two or more of the species forming the habitat group were found associated on 31 per cent of the occasions. The possibility of chance association of any two of the species in question may be calculated approximately by ascertaining the percentage of the total bird population of the area constituted by each species, then multiplying all possible combinations of these percentages, and averaging the results. By this method there would be approximately 5 per cent association due to pure chance. Thus the actual percentage of association among these species was approximately six times as great as the percentage which would be due to chance.

CONCLUSION AND SUMMARY

An analysis of the activity relations of a four-species habitat group of winter birds in western New York, consisting of the tree sparrow, the black-capped chickadee, the downy woodpecker, and the white-breasted nuthatch, indicates that all four species selected the swamp edge as a primary center of activity. However they showed some tendency to develop secondary centers of activity in the upland forest edge, and in the dwelling environs. In general the nuthatch and the downy woodpecker were more wide-ranging, while the tree sparrow and the chickadee formed the nucleus of the group.

All four species showed a marked tendency to confine their activity to the horizontal zone extending from the ground to the twenty-foot level. Approximately 81 per cent of the observed activity of the group took place between these levels. However in this case again the nuthatch was less definitely limited than the others.

The activity of these species was closely related to general weather conditions. However the downy woodpecker and the nuthatch were apparently more sensitive to gross weather changes than were the tree sparrow and the chickadee. All four species exhibited a pronounced depression in activity on completely cloudy days without precipitation, and a slight rise in activity

on cloudy days when rain or snow was falling. The greatest amount of activity took place on partly cloudy and sunshiny days. This relation was apparently entirely independent of temperature.

The total density of birds of this habitat group in the area studied was approximately 423 to the square mile. This number compares favorably with estimates of bird density in winter in other regions with similar climate.

Two or more species of the group were found associated on 31 per cent of the occasions. This is approximately six times the amount of association which would occur through the operation of chance.

ACKNOWLEDGMENTS

The writer wishes to express appreciation to Mr. F. T. Burke, Executive Secretary of the Monroe County Park Commission, for the opportunity of making this study; and to Dr. H. J. Van Cleave of the University of Illinois, for reading a preliminary draft of the paper and making valuable suggestions concerning it.

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A CORRELATION METHOD FOR ECOLOGY AS EXEMPLIFIED BY STUDIES OF NATIVE DESERT VEGETATION

GEORGE STEWART AND WESLEY KELLER

Intermountain Forest and Range Experiment Station, Ogden, Utah

Every field of scientific research had its beginning in relatively crude observations that led to the formulation of certain obvious generalizations. As each field became more thoroughly explored an increasing refinement in technique was necessary in order to discover laws or facts that were not observable by the less refined methods of the earlier investigations. One of the most important developments making for greater refinement of analysis and one which is now extensively employed in almost every field of research is the statistical method. It provides the investigator with mathematical methods of obtaining from his data much that is not obvious to the eye.

As one of the methods of statistics, the correlation coefficient has become an important tool in the analysis of many agronomic and breeding problems. It promises to become equally helpful to the ecologist in evaluating the many related forces acting upon plant associations. The importance of plant competition and soil heterogeneity on the yield of cultivated crops is well established. With range soils manifestly more variable than the better cultivated soils, and with native species subjected to differential opportunities of growth and reproduction as a result of grazing, correlation studies seem to offer, for certain problems, analytical possibilities hitherto neglected by most ecologists.

One manner of studying ecological data by the correlation method is the subject of this paper.

NATURE OF DATA USED FOR CORRELATIONS

In 1934 an inventory was made of the vegetation on the newly established Desert Experimental Range (87 sections) and of 22 sections of outside range immediately adjacent. This area, located about 50 miles west of Milford, Utah, is typical of the semidesert lands¹ of Utah and Nevada, being characterized by the northern desert shrub formation and useful chiefly for the

¹ The climate of the desert area is characterized by an annual precipitation of 6 or 7 inches occurring principally as spring rains and winter snows, with occasional summer showers, which vary greatly in frequency and amount of precipitation from year to year. Subzero temperatures usually occur during some winter nights while the summers are characterized by long periods of drought with maximum midday temperatures above 90° F. and occasionally above 100° F. Wind velocity is relatively constant throughout the year with monthly means usually between 4 and 6 miles an hour, but with a few gales reaching 15 to 30 miles an hour.

grazing of range sheep during the winter months. The primary purpose of the inventory was to ascertain the location (distribution), amount, and kind of forage then available, as a basis for planning comparative systems of grazing use of the area and as a check on a similar survey which it is planned will be made at some future time after the range has been subjected to different intensities and different periods of grazing.

The inventory was compiled from information obtained on 10,900 sample plots of 200 square feet each, 100 plots having been systematically located on each of the 109 sections. The amount of vegetation on each plot was estimated for each species by the point-observation method by which trained workers quickly attain a high degree of consistency and check very closely with each other. The data are recorded in square feet of ground covered by which is meant the projection of the crown cross-section compressed just enough to leave no open space as examined from above. The vegetational units in which the plots occurred were given a "type" designation according to the dominant species found on them. The term vegetational "type" as used in this paper refers to a single continuous area which is characterized by the relatively uniform distribution of one, two, or more prominent species named in the order of volume of forage present.

The present study arose as a by-product of this forage inventory. It is an attempt to find an explanation for the distribution of plant species by communities.

These vegetational types, about one hundred in number, differed greatly in size, including from only one to more than 500 plots. However, more than half of the entire area fell within 30 vegetational types, none of which contained less than 90 plots. The data from each plot on these 30 types provided the information used to study the relationship between species by the correlation method.

In a correlation study it is important that the investigator obtain a reasonably true cross-section of the parent population (from which he is drawing random observations), because the significance of a correlation as determined by "odds" is purely a matter of probability, and the theory of probability is based on an infinite population of normal distribution.

Most species are known to be distributed more or less characteristically in nature, but when the natural distribution is sampled by a given number of small plots (point-observation method) the size of the plot must be considered. If a species is distributed normally in nature it is likely that if the size of plot is such that the species is present in a high percentage of the plots—when a large number of plots are used, that size of plot will be found to give it an approximately normal distribution either on the basis of the number of plants or the area of ground covered, on each plot. This is likewise true of any other species which occurs on as high, or a higher percentage of the plots (which Raunkiaer, '34, calls "frequency"). However, the frequency of different species varies greatly and consequently if the size of

plot is not large enough to permit the regular recurrence of a particular species, its distribution even on a large number of plots will be skewed in the direction of zero frequency, resulting in a J-shaped curve. Also, if the size of plot is increased to include a greater number of species, the relationships between species become less intimate than in smaller plots because some of the plants are farther away from each other, thereby causing the relationship within one group to be offset by different relationships within another group on the same plot. It therefore follows that the smallest size of plot which allows a normal distribution (a high frequency) will be the most efficient as a basis for studying species relationships. This, in most cases, limits a correlation study to a few of the most abundant species within each type.

In the present study plots containing an area of 200 square feet allowed, on most of the types with 90 or more plots in each, a relatively normal distribution for two or more of the principal species. Since the area studied is characterized by a very sparse plant growth, intimate interspecific relationships are not to be expected because here the most intense relationships are probably between each plant and the moisture supply or some other force of the environment which limits its growth and spread.

CORRELATION AND ITS INTERPRETATION

Much has been written in the field of research technique concerning the measurement of correlation, that is, the extent of relationship between associated variables. Workers in many fields of scientific research understand the concept of correlation well enough to use it. It is not scarcity of information concerning correlation, but rather the slowness with which ecologists have adopted this valuable method of analysis, that warrants a few statements, principally concerning interpretation.² These statements will be limited to simple, partial and multiple correlation coefficients, which constitute the only measures of correlation employed in the present study, and which seem most likely to prove useful to ecologists generally.

A simple correlation coefficient (r) provides a relatively exact measure of the extent of the relationship between two associated variables, provided these variables are measured quantitatively, and the relationship between them is approximately expressed by a straight line³: The constant r has a range from zero (no relationship) to $+1$ or -1 (perfect relationship) but in the biological sciences perfect relationships are probably never obtained, values of .5 to .7 being counted very satisfactory and much smaller ones, when consistently reported, being useful in indicating trends. The main point is

² For methods of computation, which are purely mechanical and involve only simple mathematics, the reader is referred to references under "Literature cited."

³ If the relationship is curvilinear, that is, if it is best expressed by some curved line, the correlation ratio is a more efficient measure, while if the variables are classified in categories (as color would be) then the coefficient of contingency is used to determine the presence or absence of significant departures from independent distribution.

whether they are statistically significant as measured by accepted standards (Fisher, '30).

The closeness of a relationship is reflected in the size of the correlation coefficient, and is expressed by $100 \times r^2$ which gives the percentage of the total variability⁴ accounted for by correlation.

Every correlation coefficient is subject to a test of its significance. By significance is meant the assurance one has that there is actually a relationship between the two variables in the infinite population from which a relatively small number of random point observations have been drawn.

Levels of significance are arbitrarily placed at odds of 19:1 and odds of 99:1. A correlation coefficient is assumed to be significant when it gives odds greater than 19:1, whereas when it gives odds greater than 99:1 it is judged highly significant. It is very unlikely that a random sample showing odds greater than 99:1 will be drawn from an infinite population whose true correlation value is zero, since such a departure would occur only once in a hundred times. The size of correlation coefficient which is required, for various numbers of observations, to give odds of 19:1 and of 99:1 can be read directly from appropriate tables (Wallace and Snedecor, '31; also Fisher, '30).

Usually a third variable, or even several additional ones, influence the relationship between any two. Frequently it is desirable to hold constant the influence of these additional variables, thereby removing their influence from the correlation between the two variables being observed.

For efficient analysis of such a problem, a method is required which utilizes all of the information available and which at the same time excludes all of the influence contributed by the variables being held constant. The partial correlation coefficient accomplishes this. As regards the amount of variability accounted for and the levels of significance, its interpretation is essentially the same as for the simple correlation coefficient (Wallace and Snedecor, '31).

The above problem may be carried a step further. When the various simple correlations have been obtained, and from them the various partial correlation coefficients calculated, it may be helpful to determine how much of the variation in any one variable can be accounted for by the combined effect of the other variables. Such a result is obtained in the multiple correlation coefficient. When this constant is .85 to .95 it is assumed that under the conditions of the experiment, most of the important influences have been accounted for. If it is much smaller, that is only .50 to .60, it is highly probable that some important influences have not been considered. The interpretation of the multiple correlation coefficient itself is similar to that of the simple and of the partial correlation coefficients.

⁴ The reduction in the standard error of estimate is given by the formula $100 \times (1 - \sqrt{1 - r^2})$, this method being the one used by Wallace and Snedecor ('31). It will thus be noted that 100 per cent of the variability of one variable is accounted for only with perfect correlation ($r = \pm 1$).

THE SIMPLE CORRELATION COEFFICIENTS

Type Chrysothamnus stenophyllus-Eurotia lanata

Species relationships were studied in the present investigation on 30 plant types. More than 200 separate species combinations (correlations) were examined. To simplify the presentation, one type will be considered in some detail, after which a group study of the entire 30 types will be presented.

The type *Chrysothamnus stenophyllus-Eurotia lanata*, as is indicated by its name, is one in which *Chrysothamnus stenophyllus* is the most prominent species and in which *Eurotia lanata* is also relatively abundant. Other species found on the area in measurable quantities in the order of their abundance are: *Artemisia nova*, *Oryzopsis hymenoides*, *Atriplex confertifolia*, *Gutierrezia sarothrae*, *Ephedra nevadensis*, *Chrysothamnus nauseosus*, *Emplectocladus fasciculatus* and *Sitanion jubatum*. In addition, 8 or 9 other species were present in quantities too low to measure and were designated as showing a "trace." The quantity of current growth for the four species that were most abundant on the 182 plots in this plant type were correlated with each other in all six possible combinations, and the constants presented in table I. A care-

TABLE I. Correlation coefficients between the abundance of species numbered 1, 2, 3 and 4. The size of correlation coefficient required to give significance of 19 : 1 and of 99 : 1 is also presented

Species	(2) <i>Chrysothamnus</i>	(3) <i>Eurotia</i>	(4) <i>Oryzopsis</i>	Significance	
<i>Artemisia</i> (1).....	+.038	-.188	+.206	<i>r</i>	Odds
<i>Chrysothamnus</i> (2).....		-.459	-.243	.146	19 : 1
<i>Eurotia</i> (3).....			-.001	.190	99 : 1

ful study of table I indicates that the correlation coefficient of +.038 between *Artemisia* and *Chrysothamnus* is nonsignificant. This is shown in the columns headed "significance" where it may be seen that *r* must be at least .146 before the lowest level of significance (odds of 19:1) is attained with 182 observations for each of the two species studied. Within this type *Artemisia* and *Chrysothamnus* do not appear to bear any mutual relationship when considered in terms of their relative abundance on plots 200 square feet in area. The second correlation, that of *Artemisia* with *Eurotia* gave a value of —.188 and by reference to the levels of significance, it is obvious that this correlation approaches a high degree of significance, since it is almost as great as .190 the figure required for odds of 99:1. Size of odds does not tell anything about the closeness of the relationship between *Artemisia* and *Eurotia* but simply indicates that the chances are rather high (probably 90:1) against a correlation as large as —.188 arising by chance when 182 observations are drawn from a noncorrelated population of infinite size. It is concluded, therefore, that there is a real negative relationship between *Artemisia* and *Eurotia*, that is *Artemisia* increases as *Eurotia* decreases, and vice versa.

To determine the amount of variability in *Artemisia* that can be accounted for by the variability in *Eurotia*, substitution is made in the formula $100r^2$, and an answer of approximately 3.53 per cent obtained. This may appear to be a disappointingly small amount, but it should be noted that this low percentage of variability accounted for by a significant correlation is a clear-cut illustration of the greater refinement of analysis possible by the correlation method, since a relationship of this magnitude would in all probability be far too slight for visual detection.

The third correlation, that of *Artemisia* with *Oryzopsis*, is $+.206$ which is judged as being highly significant since it is larger than $.190$ and consequently has odds greater than 99:1. It seems safe, therefore, to conclude that as *Artemisia* increases there is a small but real tendency for *Oryzopsis* to increase also.

The fourth correlation between *Chrysothamnus* and *Eurotia*, is $-.459$ which happens to be the largest value obtained on any of the types. It is interpreted as being highly significant because it far exceeds $.190$. Actually the odds exceed 10 billion to 1 but for all practical purposes odds greater than 99:1, no matter what their magnitude, receive essentially the same interpretation, namely, that the particular correlation to which such odds refer is real. This correlation, like that between *Artemisia* and *Eurotia*, indicates (because it is negative) that as *Chrysothamnus* increases *Eurotia* decreases, and vice versa. The relationship, however, is more intimate because the correlation coefficient is larger. The formula $100r^2$ shows that 21 per cent of the variability in *Chrysothamnus* is explained by the variation in *Eurotia*. These data strongly corroborate a field observation that as grazing weakens the highly palatable *Eurotia*, there is a rapid increase in *Chrysothamnus stenophyllus*.

Although not visible to the eye, a correlation that accounts for 4 per cent or only 2 per cent of the variability within a species may be important. Relationships in nature are usually the result of an intricate network of many small influences so combined as to produce great effects. Moreover, a small influence operating through a long period of time may bring about great ecologic consequences.

The fifth correlation is that between *Chrysothamnus* and *Oryzopsis* with a coefficient of $-.243$, which is also highly significant. There is a small but real negative relationship between these two species, the magnitude being such that 5.9 per cent of the variability in the volume of growth in one species is due to its association with the other species. As one increases the other decreases.

The last correlation ($-.001$), that between *Eurotia* and *Oryzopsis* is interpreted as indicating that the one species has no measurable influence on the other.

GROUP STUDY OF SIMPLE CORRELATION COEFFICIENTS

In the analysis of the correlations from all 30 plant types, as a group, the correlation between each two species is studied without regard to the type in which it occurred. All of the correlations, based on species combinations, are presented in table II and studied as a group. In table II the first cell, which represents the correlation of *Atriplex confertifolia* (heading at left) with *Aplopappus falcatus* (heading at top), contains the data — .343 (2). The figure two in parenthesis (2) indicates that two significant negative correlations (originating on separate types) were given a single or average value by the use of Fisher's z (Fisher, '31), the average value obtained being — .343. This cell, containing no other data, indicates that the relationship between *Atriplex confertifolia* and *Aplopappus falcatus* was studied on only two separate types. In the other types these two species did not occur together in great enough abundance to merit consideration.

The second cell to the right on the top row contains many more data. The information given represents a summary of correlations between *Atriplex confertifolia* and *Artemisia nova*. From the top of the cell the first figure is + .176, which represents one simple correlation coefficient and indicates that in only one type was there a significant positive relationship between *Atriplex confertifolia* and *Artemisia nova*. Immediately below this figure are the data — .251 (4) which indicate that *Atriplex confertifolia* and *Artemisia nova* gave significant negative correlations on four separate types, the value — .251 being the most appropriate average expression as determined by Fisher's z . At the bottom of the cell is a figure four in parenthesis, (4) indicating that on four additional types the correlations were not significant.

Data in each cell are all arranged in this manner. The data in the third cell (*Atriplex confertifolia* and *Aplopappus nuttallii*) indicate that only one nonsignificant correlation was obtained for these two species.

Sixteen of the cells contain similarly generalized correlation coefficients (averages of more than one simple correlation) derived by means of Fisher's z . Significance of these generalized r 's is determined by the standard error of z which Fisher shows (*Ex.'s* 27 and 29) to be rather accurate, even for small populations. The standard error of z is $\sqrt{S(N-3)}$ in which N is the number of pairs of observations from which each correlation is derived, and S represents the sum. By multiplying z by $\sqrt{S(N-3)}$ a value is obtained which corresponds to dividing z by its standard error and from Fisher's table of normal deviates (Fisher, '30, table I, in appendix) the significance of z (and consequently of the generalized r equal to z) can be determined directly, as odds. The use of z introduces a correction for r which has increased importance as the true correlation value of the population being sampled advances from zero toward + 1 or — 1. As the real value of r increases, the distribution of r produced by repeated random samplings deviates increasingly from a symmetrical distribution about the true value. This occurs because r is limited to ± 1 . However, z is limited to \pm infinity and gives a practically nor-

mal distribution around the true value of r , regardless of the magnitude of r . Fisher explains the use of z in considerable detail and gives a table (V, B) from which values of r can be changed to z , and vice versa.

All of the generalized r 's in table II are significant by odds greater than 99:1. Inspection of the table shows that 17 species combinations (represented by cells in the table) each contain more than one significant correlation. Of these 17 there were only 5 combinations in which different types gave both positive and negative (significant) correlations. Of the 59 significant individual correlations from which the generalized r 's are derived, only 6 carried contradictory signs. This leads to the conclusion that when 2 species are found to show a significant relationship, that relationship tends strongly to be either plus or minus. The correlations of *Atriplex confertifolia* with *Oryzopsis hymenoides* illustrate this point, there being 8 significant values, all of which are positive. The average value, +.237, can be interpreted as being the most probable measure of the correlation between these two species on those parts of the entire area where correlation exists. That there were 9 nonsignificant correlations in addition is not surprising since there are undoubtedly various degrees in the completion of the adjustment between these two species. Since there was not a single contradictory significant correlation from 17 trials, the evidence is very strong that these two species tend, under conditions existing on the experimental range, to decrease together or to increase together, that is, they are ecologic commensals. This statistical evidence, borne out by field observations on much larger areas, demonstrates in a large measure the use and the reliability of correlation as an ecologic method.

The relationship of *Atriplex confertifolia* is shown to *Eurotia lanata* and to *Hilaria jamesii*. Of 12 correlations between *Atriplex* and *Eurotia* 8 were significant, of which 6 were positive and 2 negative. Of 12 correlations between *Atriplex* and *Hilaria* only 1 was significant. There seems without doubt to be a distinct correlation between *Atriplex* and *Eurotia*. On the other hand, 12 attempts failed to amass strong evidence of such a correlation between *Atriplex* and *Hilaria*. Field observations have made clear that in some stages of ecologic adjustment *Eurotia* grows naturally in a mixed community with *Atriplex*, under which conditions positive correlations would be expected and 6 such were found. In certain other stages of adjustment and on areas much less extensive in area, *Eurotia* tends to occur without any other shrubs in the plant community. Grazing data show that the highly palatable *Eurotia* when injured permits the invasion of *Atriplex*. In such cases the correlation would be negative, and two such were obtained.⁵ Re-

⁵ Two species may under one degree of adjustment give significant positive correlations, under other degrees of adjustment negative correlations. During the transition from positive to negative, or vice versa, there is a period when values near zero are to be expected. It seems reasonable therefore to rule out of consideration for a given moment the nonsignificant values of r .

lationships, as those between *Atriplex* and *Eurotia*, well-established by grazing data, show how accurately and with what discrimination the correlations describe the relationship. The ecologic conditions that make *Atriplex* and *Eurotia* commensals in one case and vigorous competitors in another are not sufficiently studied, but there is no doubt that these two conditions exist. The correlation study definitely indicated its capability to find them both.

Grazing observations, which are new on the northern desert shrub range, are not as yet adequate to permit passing judgment on the general lack of relationship between *Atriplex* and *Hilaria*. From the relationships previously cited where moderately numerous available field observations show a close correspondence with correlation data, there seems strong reason to accept the correlation data in other cases. At any rate correlations can be used effectively to ferret out clues to be followed by biologic observations when they can be made.

Since the survey was conducted primarily to obtain a forage inventory and not for raw ecologic data, many of the association groupings by paired species naturally occurred a limited number of times, too few for great reliability. It is obvious that one or two correlations are not enough to warrant any general conclusion. Several cases in which 3 or more correlations perhaps suggest moderately definite relationships are as follows:

1. *Bouteloua gracilis* and *Hilaria jamesii* seemed to be natural competitors, or have not advanced beyond that stage in their present adjustment.

2. *Artemisia nova* and *Oryzopsis hymenoides* may be commensals but not strongly so.

3. and 4. *Chrysothamnus stenophyllus* and *Oryzopsis hymenoides* seem to be strong competitors, which is likewise true of *Hilaria jamesii* and *Sporobolus asperifolius*.

5. A weak competitive relationship seems to exist between *Gutierrezia sarothrae* and *Oryzopsis hymenoides*.

Several other suggestions of ecologic relationship occur in the table but they are less definite because of the small number of correlations bearing on them. For example, the two high negative correlations between *Oryzopsis hymenoides* and *Sporobolus asperifolius* ought not to be ignored nor the two similar ones between *O. hymenoides* and *Aplopappus falcatus*. Finally any significant correlation coefficient, especially a rather high one suggests further study. To indicate just one from several cases, the coefficient of +.418 between *Eurotia lanata* and *Sitanion jubatum* indicates the likelihood that these two species are commensals.

PARTIAL AND MULTIPLE CORRELATIONS

For the entire area, which has just been considered, only about two-fifths of the simple correlations were judged significant (odds above 19:1) and on the average, only about two-fifths of the correlations from each type were

significant, though all were significant in some types and none in others. From this it would be expected that partial and multiple correlations would be nonsignificant on many types, and significant in some.

The highest correlations are the most profitable because they reflect what might be regarded as the maximum amount of influence to which any one species is subjected by others. Thus, in determining partial and multiple correlation coefficients calculations were made from only those vegetational types where a large proportion of the simple correlations were significant.

The simple, partial and multiple correlations from one such type, together with levels of significance are presented in table III.

TABLE III. *Simple, partial and multiple correlation coefficients, and level of significance, for a single type containing 120 plots*

Species	Multiple correlations	Simple and partial correlations		
		<i>Bouteloua gracilis</i> (2)	<i>Eurotia lanata</i> (3)	<i>Ephedra nevadensis</i> (4)
<i>Atriplex confertifolia</i> (1)	$R_{1.234} = .4285$	$r_{12} = -.252$ $r_{12.34} = -.1791$	$r_{13} = +.329$ $r_{13.24} = +.2379$	$r_{14} = -.285$ $r_{14.23} = -.2336$
<i>Bouteloua gracilis</i> (2)	$R_{2.134} = .3240$		$r_{23} = -.274$ $r_{23.14} = -.2104$	$r_{24} = +.075$ $r_{24.13} = -.0249$
<i>Eurotia lanata</i> (3)	$R_{3.124} = .4031$			$r_{34} = -.213$ $r_{34.12} = -.1339$
<i>Ephedra nevadensis</i> (4)	$R_{4.123} = .3186$			
Levels of significance	Odds	Simple (r)	Partial (r)	Multiple (R)
Lowest significant	19 : 1	.180	.182	
Lowest highly significant	99 : 1	.235	.238	.288

The four simple correlations ($r_{12} = -.252$, $r_{13} = +.329$, $r_{14} = -.285$ and $r_{23} = -.274$) are highly significant (odds greater than 99:1), the fifth ($r_{24} = +.075$) is nonsignificant, and the sixth ($r_{34} = -.213$) falls about half way between odds of 19:1 and odds of 99:1, permitting a considerable degree of confidence in its significance. The first partial correlation in table III, $r_{12.34} = -.1791$ falls just under .182 and consequently is judged nonsignificant, though actually it may be regarded as of possible significance. The second and third are quite highly significant (the odds are just under 99:1) and the fourth falls about half way between odds of 19:1 and 99:1. The last two are nonsignificant. None of the partial correlation coefficients are so high as the corresponding simple correlations, but this re-

lationship is not necessarily to be expected. It is important, however, that in not a single case where partial correlation coefficients were determined was the value obtained appreciably larger than that of the corresponding simple correlation. This condition may be interpreted as meaning that distinctly stronger relationships than those obtained by simple correlation were not being concealed by the various interrelationships, and that since the correlations were not very large a considerable part of the total influence causing the variation in abundance of each species has not been accounted for.

The multiple correlations in table III all surpass the highly significant level, indicating that each species is considerably influenced by the combined effect of the three associated species. The extent of that influence ranges from 10 per cent to just under 20 per cent.

For the several types from which multiples were determined the largest value obtained was $R\ 3.1245 = .5543$, from a type designated *Atriplex confertifolia*-*Oryzopsis hymenoides*-*Eurotia lanata*. This coefficient is interpreted as indicating that about 30 per cent (R^2) of the variability of *Eurotia lanata* (3) was due to the combined influence of *Atriplex confertifolia* (1), *Artemisia nova* (2), *Oryzopsis hymenoides* (4), and *Sitanion jubatum* (5). Such a figure indicates that while the influence of these species on *Eurotia* is not exclusively predominating, it is still very important.

MEASURING THE INFLUENCE OF SOIL HETEROGENEITY

Another sort of statistical analysis to which agronomists have been forced in order to interpret data in a reliable fashion is that of measuring soil heterogeneity, first worked out about 20 years ago by Harris ('15). He showed that the soils of even cultivated fields selected for experimental purposes because of their great apparent uniformity were highly heterogeneous. Small areas varied so widely in crop yield, that these differences had to be taken into consideration in determining relative yielding ability of competing crop strains, or the effect of fertilizer treatments.

To measure soil heterogeneity the correlation coefficient is used to bring out the similarity between immediately adjacent small areas which, however, differ considerably from other small areas some distance away. On the most uniform cultivated fields selected for experimental work, soil heterogeneity was found to give coefficients of correlation of about $+ .4$, although many fields give much higher values. Coefficients (Harris, '20) above $+ .8$ were reported for corn yields on $\frac{1}{10}$ -acre plots.

The problem of determining soil heterogeneity on the desert is not so simple as in cultivated fields because in the mixed native plant populations on the desert, relationships between species have been found to yield significant correlations. However, a preliminary study of soil heterogeneity on one vegetational type has yielded some striking data. The plant community on which this one study was made consisted of the following species with the

corresponding percentage of the total plant cover occupied by each: *Eurotia lanata* 53 per cent, *Atriplex confertifolia* 36 per cent, *Hilaria jamesii* 8 per cent, *Oryzopsis hymenoides* 3 per cent, and about a dozen other species occurring only as traces. Since *Eurotia* and *Atriplex* constitute 89 per cent of the total plant cover of this type, these two species were studied in relation to each other and in relation to soil heterogeneity. Rough data for a soil heterogeneity study for each of the two species were obtained by counting the number of plants of each species. To these data Harris' method for calculating a heterogeneity coefficient was applied. *Eurotia* gave a heterogeneity value of $+.603$ while *Atriplex* gave one of $+.476$. These are interpreted as being the expressions of heterogeneity measured by each species, uncorrected for competition between them with other species. The correlation of *Atriplex* and *Eurotia* on this type gave a coefficient of $-.344$. An analysis by partial and multiple correlation is presented in table IV. The importance

TABLE IV. Simple, partial and multiple correlation coefficients measuring the various relationships between *Atriplex*, *Eurotia*, and soil heterogeneity. All values are highly significant

Variable	Multiple correlations		Simple and partial correlations			
	R	% Variability accounted for	(2) <i>Eurotia lanata</i>		(3) Soil heterogeneity	
			<i>r</i>	% Variability accounted for	<i>r</i>	% Variability accounted for
(1) <i>Atriplex confertifolia</i>	$R_{1.23} = .9232$	85.	$r_{12} = -.344$ $r_{12.3} = -.8995$	12. 81.	$r_{13} = +.476$ $r_{13.2} = +.9124$	23. 83.
(2) <i>Eurotia lanata</i>	$R_{2.13} = .9372$	88.			$r_{23} = +.603$ $r_{23.1} = +.9284$	36. 86.
(3) Soil heterogeneity	$R_{3.12} = .9451$	89.				

of soil heterogeneity is reflected in every partial and multiple correlation. In the simple correlation $r_{12} = -.344$, 12 per cent of the variability of one species is attributable to variation in the associated species. With the influence of soil heterogeneity held constant ($r_{12.3}$) the correlation is increased to $-.8995$ representing 81 per cent of variability. Soil heterogeneity alone has increased the quantitative measure of the associated relationship between *Atriplex* and *Eurotia* by 69 per cent, leaving a total of only 19 per cent unaccounted for.

The estimation of soil heterogeneity by variation in a single species, uncorrected for its relationships with other species, proved to fall considerably short of the actual heterogeneity as reflected in the partial correlations $r_{13.2} = +.9124$ (in contrast with $r_{13} = +.476$) and $r_{23.1} = +.9284$ (in contrast with $r_{23} = +.603$). The multiple correlations indicate that from 85 to 89 per cent of the variation in each variable is accounted for by

its relationship with the two associated variables. Most of the remaining unexplained variation may be tentatively assigned to: (1) the unmeasured influence of *Hilaria* and *Oryzopsis*, comprising 11 per cent of the vegetation, and (2) variations in the intensity of grazing on *Eurotia* on the area sampled. The corrected measures of heterogeneity may appear to be extremely large, but when one considers that those species have had decades in which to express soil variation by their distribution and abundance, together with the fact that competition between species exercises a selective influence, there is no adequate reason for concluding that the values reported are abnormally high. This small preliminary study is not expected to measure so complex a relation with final accuracy, the present objective being to point out that ecologists had paid little attention to soil heterogeneity and to indicate its great influence and the method of measuring it. More extensive studies are necessary before general conclusions as to the measured influence of soil heterogeneity can be drawn. The influence of heterogeneity, in the present preliminary study, appears to be very important, but it must be remembered that 89 per cent of the total plant cover consisted of *Atriplex* and *Eurotia*. With an ordinary mixed plant distribution such as occurs in many types, it would probably be necessary to obtain the various relationships for four or five species in order to explain as much variability as has been found in the above example.

STATISTICAL METHOD IN ECOLOGY

Two advances of real consequence would at one stroke be made by ecology if its workers were to apply the statistical method: (1) plans for conducting surveys or experiments would be greatly improved and (2) quantitative data would be accumulated systematically, permitting a strong superstructure to be reared on the present qualitative basis. The statistical method requires that an experiment embody in its original design provision for obtaining such data as will make adequate analysis possible. This means careful planning prior to the beginning of the investigation, especially to insure the provision of check plots or check plants; of random, or at least representative, samples; and of replication of treatments—all required in order to assure measures of reliability.

Ecology must soon become a quantitative science if its advance is to be unimpeded. In a thorough understanding of the problems of livestock ranges, for example, the strength of the forces tending to injure vegetation, and the relative value of different practicable means available for building it up, require the unraveling and evaluating of many strands in the intricate web of natural and imposed influences. Descriptive information alone is sure to be inadequate, whereas on many of the problems correlation analysis and other statistical methods will yield quantitative measurements and make weighted deductions possible.

DISCUSSION

In the present study an attempt has been made to determine, by correlation, the various relationships between species on the northern shrub desert of western Utah. When the variables employed are limited to species the values obtained are consistently rather small, over half of the total being nonsignificant. The other coefficients, however, are so definitely and so consistently significant as to leave little doubt that a major species is distinctly influenced as a result of the presence of the others.

Partial correlation did not strengthen the relationships as measured by absolute size of coefficients. Multiple correlations indicated that probably not to exceed 30 per cent of the variation in any one species was accounted for by variations in the associated species. In some of the types examined, this figure fell below 10 per cent. Although 10 per cent of the variability is a very significant quantity, it leaves so much unexplained that it is obvious some very significant factor or factors have not been taken into consideration.

When all of the significant correlations between each pair of species were grouped, regardless of type, as was done in table II, there was a marked tendency for all the coefficients in each group to have the same sign. The relationships, therefore, between any such pair of species are not randomly distributed, indicating that definite factors of considerable constancy are causing these relationships. The complete interpretation for this fact cannot be established at the present time, although several likely explanations suggest themselves, each having something to do with the intensity of competition.

In a search for additional factors responsible for variation in the distribution and abundance of plants, use was made of the soil heterogeneity influences. Data from a preliminary study indicate the tremendous influence of heterogeneity in such a conclusive manner as definitely to indicate that ecologists can no longer afford to neglect this powerful factor.

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THE ECOLOGY OF A LAWN

WILLIAM R. VAN DERSAL

Soil Conservation Service, Washington, D. C.

In April, 1931, a lawn was started at the University of Pittsburgh, covering approximately six acres and surrounding the Cathedral of Learning. Sections of about one acre each were prepared and seeded in six different plantings. In May, 1932, the last planting was completed, and in 1933 the author was called upon to examine the lawn and to make reports upon it. The examination was instituted to determine whether the remainder of the land should be seeded with the same grasses and fertilized with the same materials as were used in the earlier plantings.

Because of the time which had elapsed between successive plantings, and the fact that each planting was given exactly similar treatment, the author felt that a useful survey might be made to discover just what happens to a lawn of this more or less usual type after it has been started.

SOIL CONDITIONS

The area leveled and graded was a very heavy clay. On this was laid an eight-inch layer of top soil and on top of this an "icing" layer of compost 3-4 inches thick. The icing layer was composed of two parts by volume of "German peat moss," one part of well rotted manure and one part of top soil. The organic content (determined by incineration of dry sample) and the percentage of water held (determined by saturating sample, then drying it to constant weight at 110° C.) for the various components of the icing layer are shown in table I. These figures are based on results obtained from analysis of ten random samples of each material. In the same table there are similar figures for a sample of the compost, before and after two years of service as a lawn producer. This figure is based on 15 samples taken at in-

TABLE I. *Amounts of water and organic material in components of lawn soil and in compost used*

Sample	Percentage of water		Percentage of organic material
	Based on wet weight	Based on dry weight	
German peat-moss.....	75.5	308.	78.0
Well-rotted manure.....	75.6	310.	24.0
Top-soil.....	30.4	43.	3.0
Compost as used.....	47.8	91.	7.2
Compost after two years.....	43.2	90.	5.4

tervals over a considerable area of lawn to a depth of three inches, which was a little less than the actual thickness of the icing layer at the time the determinations were made.

The loss in organic material in two years was thus 25 per cent and, assuming a constant deterioration (which probably does not occur), this would mean a yearly loss averaging 12.5 per cent. This is not to be understood as indicating that the yearly loss will continue at the same rate year after year. On the contrary, more recent determinations show that the organic content of the compost layer actually begins to increase and continues to do so until a constant figure is reached, which persists under the conditions of partial removal of clippings, watering with care, use of chemical fertilizers and bone-meal as later indicated. The drop in organic content during the first two years is probably due to considerable decomposition of the peat moss, coupled with the fact that the lawn clippings were removed continually before root development and death could stop the drain of organic material loss.

Because the organic content began to increase after two years, it is apparent that on a lawn of this type there is no need to supply more organic material in the form of manures, peat-moss or peat. Further, the organic content would probably have remained either nearer the original figure or would have increased if the lawn clippings had been permitted to remain on the grass after cutting. It may also be noted that seasonal fluctuations in the organic content may be observed. The material increased (to a figure during one season as high as 16 per cent in the upper two inches) in the winter when decomposition is necessarily slower, later decreasing during summer when bacterial activity increases. The figures for organic material present often show a sudden drop within a short time after such a fertilizer as bone meal is added. This is due probably to increased bacterial activity.

The lawn was fertilized with Milorganite, raw bone meal, and ammonium sulfate. All of these fertilizers would tend to make the soil more acid. Poisons, such as lead arsenate and mercurous and mercuric chloride were added from time to time to control Japanese beetle larvae, sod webworm, and the various fungus diseases which attack lawn grass.

The amount of water held by the lawn soil is important. In Pittsburgh there is nearly always very dry weather for a month or more during the late summer. This period is critical for plants which are not watered. If there were substances present in the soil which would aid in conserving water, the critical, dry period might be safely weathered. For this reason, the use of the German peat moss (a partially decayed sphagnum moss from peat bogs) was recommended to be continued.

At the time the study was being made, other materials were tested for percentage of water held, organic content, and pH, but no other material held as much water as the German peat moss. The attention of the writer was also called to the fact that cultivated peat (obtained by plowing green crops into old peat material and thoroughly mixing the resultant compost) might

be more useful for a lawn as the organic content of the soil would remain higher for a longer time since cultivated peat is in a more advanced state of decomposition than other peat products. Thus after peat has passed its initial stage of rapid decomposition, the substances present in it decay more slowly. Cultivated peat has reached the slow stage and consequently, when it is applied to soil, the organic content might be expected to remain more nearly constant, but when determinations were made, and it was seen that the organic content of cultivated peat was, relatively speaking, unnecessary, the superior capacity of German peat moss to hold water decided the question. The experiments here described lasted only over a three-year period, but according to Dr. J. W. White of the Department of Agronomy at Pennsylvania State College (in a lecture delivered at the Pennsylvania Greens-Keepers' Conference, 1933) there is an increase over a sixty-year period in the organic content of soils underlying sod. The reason for attempting to ensure a stable, high organic content over a shorter period is thus not apparent.

GRASS USED

As originally planted, four kinds of grass were used to sow the lawn. These were, Pacey's English rye (*Lolium perenne*), redtop (*Agrostis alba*), Kentucky bluegrass (*Poa pratensis*) and bent (*Agrostis canina*). The mixture of the seed of these species (and it is recognized that many strains of each were very likely present) contained 50 per cent by weight of bluegrass, 30 per cent of bent, 10 per cent of redtop and 10 per cent of rye. The rye was intended to shade the slower growing grasses, and to anchor the soil. The other three species were used because they were good hardy types of value for a fine lawn.

The fact that a mixture was planted (and usually is in most lawns) was of interest since it is known that fungus diseases travel faster and do much more damage in pure, or nearly pure stands of one species than in mixed stands. No disease which has appeared in the lawn has traveled with anything like the rapidity nor done relatively as great damage as disease in other lawns maintained by the University. For instance, certain *Fusarium* wilts have occasionally attacked young patches of the Cathedral lawn, or "Brown Patch" has rarely caused very slight spotting, but neither disease has spread far. In a lawn, however, composed nearly exclusively of Chewing's fescue, in spite of careful poisoning with mercurous and mercuric chloride before and after the epiphytotic in addition to the use of Bordeaux mixture sprayed on, nearly three-quarters of the grass on a 60,000 square-foot field was killed.

It might be mentioned that the role of "protector" for the rye is rather offset by certain disadvantages it possesses; these later caused the author to recommend that its use be discontinued. This recommendation was based on the facts, that while rye grows rapidly immediately after germination giving (1) a quick stand of grass, (2) shade for slower-growing grasses, and (3)

quick anchorage of the soil, it produces great unevenness of the lawn surface and freezes back, developing ugly brown patches. The quick stand does not seem to be necessary as the other grasses come up only a few days later and shade each other. Anchorage of the soil is unnecessary if the soil has been properly prepared and deeply cultivated so that water from sudden showers will percolate downwards more quickly than it will run off. In the author's experience, very steep slopes prepared for lawns will never show water-gullies nor slides, if the soil is loose and cultivated to a depth of 12 inches; whereas similar slopes cultivated 6-8 inches deep will be deeply gullied by the same shower. Finally, on a lawn planted to fescue and a little rye, after a so-called cloudburst just when the rye was one-half inch high, the rye quite failed to anchor either the soil or itself and was very badly washed out.

THE HYDROGEN-ION EFFECTS

It soon became apparent that repeated sampling of the soil for pot cultures, chemical analysis, and determinations of water-content would scarcely be practicable. Aside from the difficulty, labor, and disturbance of the lawn by such methods (if large samples were taken) the more notable ways of controlling the lawn from the laboratory all had drawbacks which precluded their use, except perhaps, under unusual conditions. The determinations of plant foods available to the plant by means of pot cultures on the soil is attended by such difficulties as (1) necessity for taking comparatively large samples of soil out of the lawn, (2) the necessity of a rather elaborate set of experiments, and (3) the comparatively long time needed for the experiments. The author does not deny that such a method would offer very valuable data on the condition of the soil. Chemical analysis, has long been known to be of very doubtful value in indicating just how much of the materials present are actually available to the plant. Water content of the soil may be important, but lawns have been known to fail for many other reasons than for lack of water.

The author felt that the use of pH determinations in controlling a lawn might be of doubtful value. Without any question many errors have been made, and very careless work has been done in pH studies. For this reason, it was felt that some experimental work ought to be done with the grasses to confirm or contradict the studies of previous workers. The author, therefore, decided to test the practicability and usefulness of such a method of control. In doing so, he needed to know the pH range in which the grasses planted would be most likely to succeed and in which weed seeds would be most likely to fail. The reaction of the lawn soil and its variations from season to season were also probably important and knowledge whether maintaining a certain pH in the lawn soil, would tend to produce a beautiful lawn; *i.e.*, could the pH determination be used as a guide for procedure in control?

THE PH PREFERENCES OF THE FOUR SPECIES OF GRASSES

In connection with work on the Stadium lawn an experiment had already been performed to determine the optimum pH for the growth of bluegrass, and an optimum of pH 6.5 had been found. A second, less decided optimum had been noted at pH 8.0, but this was not confirmed in later experiments. The experience gained was applied to experiments on bent, bluegrass, rye, and redtop. Each of 11 containers full of chemically cleaned and washed quartz sand was planted with the four grasses. The containers were divided into four compartments (labelled A, B, C, and D) by chemically cleaned glass partitions and a section in each container was planted to redtop, to rye, to bent, and to bluegrass. Each culture was watered daily or twice-daily with Knops solution (0.1 per cent) adjusted by the use of potassium carbonate or sulfuric acid to the proper alkalinity or acidity. The pH of the solutions was determined by a quinhydrone electrode in steps of pH 0.5 from 3.5 to 7.5, and by both the quinhydrone electrode and colorimetric method (using La Motte indicators and standard solutions) from 8.0 to 9.0 (one step). Measurements were made daily of the height of the seedlings and observations on their appearance noted. The containers were all placed under one glass covering in a south window; humidity was aided by pans of water placed under the glass covering; and the temperature throughout varied from 18° to 25° C.

Results of this experiment were: a. Redtop germinated in six days at pH 5.5. This reaction appeared to be the optimum throughout the experiment. At pH 3.5 a variety of molds attacked the ungerminated seeds on the 10th day after planting. Plants at pH 4.0 and 4.5 although appearing well in the graph (fig. 1), were, throughout the experiment, yellowish, spindling, and

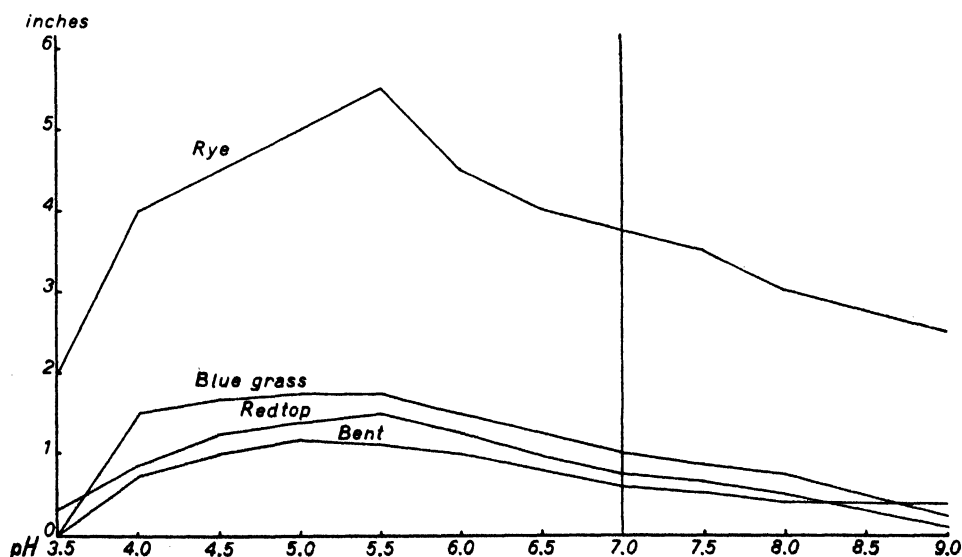


FIG. 1. Growth in inches of the four grasses at different H-ion concentrations.

weak. Plants at pH 7.0–9.0 were the same, the unhealthy condition noticeably increasing with alkalinity. The limits of the optimum for the growth of redtop were from pH 5.5 to pH 6.5. The danger point on the acid side began at 5.0 and on the alkaline side at 7.0.

b. Rye germinated in five days at pH 3.5 to 7.5 but with most vigor at pH 5.5. By 8 days germination was complete in all cultures. The pH 5.5 culture was the optimum throughout the experiment. This grass was the only one which grew at pH 9.0, but shoots at pH 3.5 were gnarled and yellowish and the tall grass in pH 8.0 and 9.0 was yellow. The optimum of this grass seemed to be from pH 5.0 to 6.5.

c. Bent germinated four days after planting at pH 5.5. This reaction seemed an optimum throughout the experiment although mold set in on the 18th day. Growth at pH 3.5 was very poor and molds soon developed. Plants at pH 9.0 were yellowish and a little spindling. Growth was satisfactory in all other pots. The optimum was distinctly at pH 5.5 until the 16th day when cultures on both sides began to rival it. The limits of the best growth of this species were from pH 4.5 to 7.5, with best growth from pH 5.5 to 6.5. The pH requirements of this plant are evidently catholic; perhaps herein lies one reason for its universal use as a lawn grass.

d. Bluegrass germinated eight days after planting at pH 5.5. This pH remained an optimum until the 10th day when it shifted to pH 6.5 which was maintained until the termination of the experiment. No growth took place at pH 3.5, mold attacking the ungerminated seeds 13 days after planting. At pH 4.0 and 4.5 shoots were yellowish and weak. At pH 5.0, although the height was less than at 6.0, 6.5, etc., the grass was in good health and color. Plants were yellowish, weak, and spindling at pH 8.0. The optimum for this grass lay between pH 5.5 to 7.0, with distinctly best growth at 6.5.

It was noted that rye grew about three times as fast as the other grasses. Bent, bluegrass, rye, and redtop germinate at nearly the same time, but rye appears in a lawn before the others because of its comparatively rapid initial growth. A lawn planted to the three grasses, redtop, bent, and bluegrass would maintain a fair level, other conditions being constant; but with a fast-growing, coarse species like rye mixed with them, the lawn will be uneven and ragged in appearance until the rye is frozen out. For this reason, and because the frozen plants later disappeared and permitted weeds and foreign grasses to come in, the author recommended that the use of rye be discontinued.

In a second experiment to check the first, bent and redtop showed identical curves and agreed almost exactly with figures mentioned above. That the check experiment, figures for which are omitted here for brevity's sake, was completely satisfactory may merely be noted.

The results obtained in these experiments indicate that for the four species of grass, other environmental factors being uniform, the optimum range of hydrogen-ion concentration may be placed as between pH 5.0 and 6.5.

This statement carries the proviso that each grass be considered separately. No experiments were performed on cultures containing mixtures of the grasses, but the work of Garner and Damon ('29) brings out several interesting points in this regard. Thus, while the "absolute" optimum pH for the growth of bluegrass may be at or near pH 6.5, in competition with other grasses, these workers show that bluegrass may persist at this reaction, but succeeds best near pH 7.8. With the soil in an alkaline condition, this grass can more than hold its own; at an acid reaction, even though it be the absolute optimum for its growth, other grasses are able to crowd it out.

The opinion has long been held that Kentucky bluegrass needs an alkaline soil, and that the use of lime is therefore to be recommended. In a communication to the writer, Dr. Edgar T. Wherry mentions that it is natural to assume that this species prefers a neutral soil since the "bluegrass region" of Kentucky is underlain by limestone, but when one makes actual tests in its native region, the bases prove to have been leached by the rain from the uppermost levels of soil, and the reaction is around pH 6, or slightly acid. The point about the whole matter is, however, that a plant may have an optimum pH range but not be found growing there because in competition with other plants it may be unsuccessful. Conversely, because a plant is found in nature, growing in soil of a certain reaction does not mean that that particular reaction is its optimum; it only means that under the particular environmental conditions, notably in competition with other plants, the plant is succeeding. The plant's pH tolerance extends over a sufficiently wide range to permit its success at a certain reaction where the competing grasses may be unable to succeed because of a lesser tolerance.

Most pH studies have only shown that certain plants do grow in soils of certain reactions but have not demonstrated that such reactions are the optima for the plants concerned. It is evident, therefore, that cataloguing plants as "acid-loving" or "alkali-loving" may be in error unless, among other factors, competition of associated plants is considered.

The pH Preferences of Weeds

The most notable contribution in this field is that of Garner and Damon ('29) whose work will be referred to again. They found during the course of their studies that by maintaining soil in an acid condition weeds were eliminated in test plots over long periods, and that under alkaline conditions, weeds were successful. They state: "The number of weeds persisting is in inverse ratio to the degree of acidity; the higher the acidity the fewer the weeds."

Many other workers (Conner and Fisher, '31, '32; Morgan, '25) have discovered the fact that weeds (dandelion, plantains, etc.) are discouraged by acid soil conditions and fostered by alkaline soil. Cox ('30), however, mentions that soil acidity is not necessarily a satisfactory cure for weeds, also

that bluegrass and clover will make a more satisfactory growth on soil in which acidity has been largely corrected.

On the lawn in question because a beautiful turf was more desired than an experiment, weeds have been persistently removed. It may be noted, however, that when the reaction approached pH 7.0, which it did locally on one plot, clover managed to get in and to become quite vigorous. On adding acid fertilizer (ammonium sulfate) and maintaining the soil as close to pH 5.5 as possible, the clover later disappeared. Clover, in this instance, was not included as a "weed." Some trouble was experienced with annual blue-grass (*Poa annua*) which apparently succeeds well in acid soil in competition with the grasses used in this planting.

On the Stadium lawn where lime is used for marking and the reaction runs from pH 7.0 to 8.5, very great difficulty with weeds was encountered. Because of the lime-lines it was almost impossible to maintain the soil at an acid reaction, and weeds are gradually taking over the field planted exclusively to Kentucky bluegrass.

It was discovered empirically that by applying twice yearly 15 pounds of bone meal and 5 pounds of ammonium sulfate per thousand square feet the soil reaction was kept very close to pH 5.6. The procedure, therefore, was to examine the soil with respect to the hydrogen-ion concentration twice yearly. If the reaction rose nearer neutrality than pH 6.5, ammonium sulfate was spread on at the rate of 5 pounds per 1,000 square feet. If the reaction remained close to pH 5.5, no fertilizer was added. During the whole time the lawn has been in existence, it has been among the most beautiful in Pittsburgh. The author feels justified, therefore, in claiming that so far, the control of the lawn by means of pH determinations has been eminently successful.

COMPETITION OF THE PLANTED GRASSES

We may now consider what happens in a lawn, knowing fairly accurately the conditions under which it has been perpetuated. To do this it is essential to know the relative percentages of the plants at the beginning, and by ascertaining the ratio of the four grasses to one another from time to time, the competition between species may be followed.

As originally planted, the percentage of seed by weight was: Bluegrass 50 per cent, bent 30 per cent, redtop 10 per cent, rye 10 per cent. The percentage by weight of seed is of no direct use in following the competition between species, therefore, for all grasses the percentage of seeds expected to germinate, was calculated. The number of seeds planted was multiplied by the germination percentage for each species to find the actual expected number of young plants. This figure was then expressed as a percentage of the total number of all species planted. Table II shows the results for the four species. It appears that the expected initial composition was 29.0 per cent bluegrass, 52.8 per cent bent, 17.6 per cent redtop, 0.6 per cent rye. This calculation is based on the number of seeds per pound given by Piper and

TABLE II. *Kinds and numbers of grasses planted*

Grass	Number seeds in one pound ¹	Per cent planted by weight	Number of seeds planted	Per cent germination ¹	Number of seeds germinating	Per cent seeds planted by numbers
Rye.....	500,000	10	300,000	85	174,000	0.6
Redtop.....	6,000,000	10	6,000,000	85	5,100,000	17.6
Kentucky bluegrass.....	2,400,000	50	12,000,000	70	8,400,000	29.0
Bent.....	6,000,000	30	18,000,000	85	15,300,000	52.8
Total.....		100	36,300,000		28,974,000	100.0

¹ Piper's estimates.

Oakley ('29). The average percentage germination of the species is taken from the same source.

It should be mentioned that the estimated percentages of germination of the seed supplied by the seedsman were far too high. Thus, bluegrass was claimed to germinate 94 per cent, bent 90 per cent, redtop 95 per cent, and rye 90 per cent. The grass planted was not tested by the author for germination inasmuch as this study was begun too late to do so. But after ascertaining such percentages on many species of grasses, the ones in this study among them, the author has noticed that seedsmen's estimates are usually about 25-40 per cent above the actual percentage, and that the estimates of Piper and Oakley are very good average percentage germination figures.

PERIODIC DETERMINATION OF THE LAWN POPULATION

It then became necessary to count the number of plants of each species of grass at successive intervals. This could be done simultaneously since the lawn as a whole was planted plot by plot over a period of two years and since the conditions had been kept constant for all plots. The writer believes that a closer approximation to the truth might be achieved by studying one plot over a long period, taking counts at intervals but under the circumstances of the study, this was not possible.

Identification of the different species in vegetative condition was difficult. Fortunately, the University had been growing sample plots of 24 species of grasses and by identifying these by means of inflorescence (part of each plot having been allowed to go to seed), then studying the vegetative characters, the author gained enough experience to attempt the identification of the vegetative samples taken from the Cathedral lawn. Use was also made of keys developed by Piper and Oakley ('29), Carrier ('17), and a paper by Piper ('31). Garner and Damon ('29) have mentioned that it is not possible, in disentangling a piece of sod to determine the number of plants which it contains if the grasses are creeping types. In their studies they relied on esti-

mates, feeling that if counts had been made, local patches of weeds would have been missed, results would have been according to numbers of plants without regard to the area they occupied, and that even if counts had been possible, the taking of large samples would have destroyed their plots. But in this study, the writer decided that counts were possible if certain conditions were observed.

First, each erect shoot, regardless of stolon attachment, was counted as a unit. Second, estimation would be difficult since the similarities between redtop and bent in vegetative condition were striking and the grasses were difficult to separate except under a lens. Third, since the planting was well-mixed, and the plants found to be well-mixed also, counts made on numerous small samples containing several thousand shoots were considered truthful indicators. Fourth, under the circumstances, the size of sample taken would scarcely affect a plot nearly an acre in area. Counting was therefore entered upon with expectancy of securing significant results. Since the percentages determined by this method agree rather well with the results of Garner and Damon, the author feels justified in having adopted it. Table IV shows, in summary, how the percentage of each grass varied from the time of planting (cf. table III) to three years later.

A consideration of these figures would indicate that in the lawn, bent has been more successful than the other grasses. Originally present in the mixture to the extent of approximately 53 per cent, it increased almost immediately to approximately 73 per cent. This increase in numbers of shoots is obviously connected with the successful stoloniferous habit. Bluegrass has decreased from about 29 to about 14 per cent. Redtop decreased from about 18 to about 10 per cent. Rye apparently increased, but as a matter of fact as it freezes back each winter, permitting the other grasses to encroach upon it, it has nearly disappeared. In the spring a year later (1934) it was very rare anywhere in the lawn, and by fall it had disappeared in the older plots.

What has happened then, is that bent has increased in number of shoots at the expense of the other grasses, one of which (rye) was killed by frost. The other two (redtop and bluegrass), even though they too have stolons, have been unable to compete, under the conditions outlined, with bent. These results are in good agreement with those of Garner and Damon ('29), who worked with the Rhode Island strain of bent.

In this study, it may be noted that the amount of bent in the turf appears to be around 73 per cent. That this high percentage of bent is rather directly connected with the hydrogen-ion concentration of the soil is indicated in table III where a decrease of H-ion concentration appears to be connected with the decrease of the bent and the increase of the bluegrass and redtop. This correlation also occurred in the study of Garner and Damon ('29) where bent of the Rhode Island and Velvet strains formed more of the turf as the soil became more acid. It must be stated that the increase or decrease of bent under competition is *correlated* with increase or decrease of H-ion concentra-

TABLE III. *Percentage composition of lawn plots at different times*

Age of planting	Rye	Redtop	Blue-grass	Bent	Clover	Remarks
Original planting ¹	0.6	17.6	29.0	52.8	0.0	
Original planting ²	0.8	17.0	33.7	48.7	0.0	
24 weeks.....	3.1	11.7	10.2	74.8	0.0	
25 weeks.....	2.8	7.2	15.3	74.6	0.0	
170 weeks.....	trace	19.0	30.7	47.0	3.3	Plot permitted to become alkaline
172 weeks.....	6.4	12.6	13.7	67.1	0.0	
173 weeks.....	0.3	7.8	18.6	73.3	0.0	
177 weeks.....	trace	8.1	10.9	75.0	0.0	
Average.....	2.5	9.5	13.7	72.9	0.0	Omitting the figure for 170 weeks

¹ Piper's estimate.² Seedsmen's estimate.

tion. This must not be taken to denote that the increase in H-ion concentration *causes* the change inasmuch as the reasons behind the correlation are not known.

In this study, the "equilibrium" between the grasses was reached very shortly after planting. Garner and Damon ('29) mention that there is a close general correspondence between the estimated composition of the plots in 1916 and 1928. Thus, in their studies, equilibrium was maintained for 12 years without change. All this would lead one to believe that a lawn flora arrives very quickly at an equilibrium indicated by (but not necessarily depending upon) the pH of the soil.

The practical implication of the determinations on percentage composition of the turf may therefore be as follows:

1. If the pH of the soil is to be maintained at a constant figure, a calculation of the amounts of seed needed in a mixture can be made.

2. Regardless of the percentage composition of grasses in a planting mixture, the lawn grasses will arrive at an equilibrium which is affected by the reaction of the soil and for pH 5.6, this is shown in table IV. This is true within the limits of experiments already studied, but how far the amount of any one grass may be decreased before it may not be able to increase and reach its normal equilibrium is not known.

3. It appears true, however, that a comparatively expensive seed such as bent need not be planted in full (calculated) amount in a mixture since it will eventually increase to an equilibrium with other grasses. This may effect a saving in initial cost.

4. If the equilibrium in a mixture for any reaction is known, then to at once achieve a lawn in equilibrium, the calculated amounts of seed must be planted in the beginning. By so doing, competition is eliminated and, the-

TABLE IV. *The initial and eventual percentage of the grass species*

Grass species	Percentage of seeds planted (by weight)	Percentage of seeds planted (by numbers)	Percentage present after competition (by numbers)	Percentage of seeds desired (by weight)
Rye.....	10	0.6	0.0	0.0
Redtop.....	10	17.6	10	8
Bluegrass.....	50	29.0	14	34
Bent.....	30	52.8	73	58

oretically at least, the energy consumed by the grasses in the struggle to supplant each other may be conserved. Many implications may be seen there, such as the conservation or waste of plant foods, etc., but such questions need a firmer foundation to be seriously considered.

The author wishes to thank Dr. E. H. Graham and Mr. M. G. Netting of the Carnegie Museum, for their helpful criticism and advice. He is also grateful to Dr. H. C. Hicks, of the Carnegie Institute of Technology, Department of Mathematics, for checking the calculations. It should also be noted that without the generous cooperation of Mr. Edward McLain of the Department of Buildings and Grounds of the University, the study could not have been pursued.

SUMMARY AND CONCLUSIONS

1. On a lawn of the type here described, there is no necessity for supplying more organic material, since the organic content of the soil increases, after a 25 per cent decrease, to a higher figure than the initial one.

2. The optimum soil reaction for rye, redtop, bluegrass and bent lies between pH 5.0 and 6.5, when the grasses are grown separately.

3. Competition of grasses planted in mixtures may materially change the reaction at which one or the other of the species succeeds.

4. In mixture of bent, bluegrass and redtop, in an acid condition of the soil (*i.e.*, pH 5.6), bent succeeds at the expense of the other grasses. At an alkaline reaction, bluegrass succeeds at the expense of the others.

5. A reaction kept near pH 5.5 excludes clover; when the reaction reaches or passes pH 7.0, clover successfully crowds out competing grasses such as bent, bluegrass, and redtop.

6. A lawn may be controlled by the maintenance of a certain reaction range; a very successful one, discounting all other factors, may be had by holding the soil near pH 5.5, using bent, bluegrass, and redtop.

7. In a lawn planted to a mixture of grasses, the species will reach an equilibrium (climax) correlated with the reaction of the soil. The more acid the soil, the more bent and less redtop and bluegrass will be present; the more alkaline the soil, the more bluegrass and redtop and the less bent will be present.

8. With the soil showing a reaction of pH 5.6 in a region where frosts are frequent, a lawn composed of bluegrass, bent (South German), rye, and red-top will arrive at an equilibrium almost immediately wherein bent will be present to the extent of 73 per cent, bluegrass to the extent of 14 per cent, redtop to the extent of 10 per cent, and rye to the maximum extent of 3 per cent. Rye will later, on account of freezing, totally disappear.

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REVIEWS

ZOOPLANKTON ¹

Professor Rylov of the Academy and of the State University of Leningrad writes this XVth volume of Thienemann's *Die Binnengewässer*. It is an introduction to the systematics and ecology of the animal limno-plankton with special reference to that of mid-Europe. Although thus restricted by title it is nevertheless widely useful in all north temperate latitudes, because of the cosmopolitan content of the limno-plankton of these latitudes. The volume is fittingly dedicated to the late Dr. Einar Naumann, Director of the Aneboda Laboratory in Sweden.

The work falls into two major parts; the first briefly deals with the concept of plankton and its subdivisions, adaptations to the plankton environment, seasonal and local form changes, nutrition, vertical and horizontal distributions, and geological relations; the second, more extensive part is a systematic presentation of the Protozoa, Rotifera, Cladocera, and free-living Copepoda, with brief notes on other groups. There are 38 pages of bibliography, and good indexes.

The main value of the work is in its treatment of the Rotifera and Crustacea in which the content and illustrations are more extensive. The treatment of the Protozoa is fragmentary and wholly inadequate. The author does not adequately follow the code of nomenclature and utilizes a quadri-nomial system of nomenclature with genus, species, subspecies (used in various senses) and variety—a procedure which in the hands of various investigators with irreconcilable ideas of the application of these categories inevitably leads to a systematically terrifying maze of synonymies.

The author's figures showing his interpretations of seasonal and local form changes will be helpful to other workers on rotifers and cladocerans. The abundant illustrations will be of great aid to beginners in the identification of animals of the fresh water plankton. The subject matter in this field is really too extensive for one volume and too intricate and complex for one specialist.

CHARLES A. KOFOID

UNIVERSITY OF CALIFORNIA

BIOLOGICAL EFFECTS OF RADIATION ¹

This treatise, prepared under the auspices of the committee on radiation of the National Research Council, represents the collaboration of forty-three

¹ Rylov, W. M. 1935. *Das Zooplankton der Binnengewässer*. xii + 272 pp., 30 pls., 16 figs. in text. *Schweizerbartsche Verlagsbuchhandlung, Stuttgart*.

¹ Duggar, B. M., and others. 1936. *Biological Effects of Radiation*. Vol. I, pp. 1-676; Vol. II, pp. 677-1343. *McGraw-Hill*. \$12.00.

authors, each of whom has had sufficient experience in the particular field of research he represents to be regarded as an "authority."

Chapters 1-5 and 7 deal with the physics of light. Chapter 7 also treats of photochemistry. While concise, the exposition of the physics of radiation, particularly in chapters 1 and 7, does not sacrifice elementary considerations to brevity. To one having a background of only general physics it will serve as a guide to the more subtle aspects of radiation theory.

Much of the discussion, as would be expected, deals with radiations of little, if any, interest to ecologists. The well-marked effects of X-rays and of ultraviolet of wave-length 2800A and shorter has resulted in a relatively great exploitation of these fractions of the electromagnetic spectrum in biological experimentation.

In those sections of the compilation which deal with conditions organisms may normally encounter, the greater space is given to consideration of the effects of visible light, ultraviolet and infrared on plants. The lesser amount of space devoted to animals is, of course, the fault of zoologists in general and not of the compilers. In the field of animal ecology the chapter on vitamins by C. E. Bills, that on motor responses of animals by Mast and to some extent the chapter by Heilbrunn and Mazia on the general effects of radiation on protoplasm will be of interest.

The treatment is complete, *i.e.*, it considers all known radiations for which biological effects have been demonstrated. There is, for example, an interesting exposition by Hollaender of the present status of research on mitogenetic rays.

To the ecologist who attempts to take into account (as he frequently is compelled to do) the part solar radiation plays in the economy of organisms this work will be of invaluable assistance as a source of reference for means of measurement (Ch. 4), the physics of sunlight (Ch. 5), and as a guide to the most carefully controlled experiments on the biological effects of radiation. Its extensive bibliographies, covering literature through 1934, taken alone make the book well worth having at hand. The citations, while professedly not complete, are ample indices to the important publications in the various fields covered by the compilation.

H. F. STROHECKER

UNIVERSITY OF CHICAGO

CAMEL-CRICKETS ¹

In this work Hubbell has presented a long needed comprehensive treatment of a genus on which the literature has been in a highly unsatisfactory state. Of the eighty-nine species and geographic races recognized forty species and four races are described for the first time. Over seventeen

¹ Hubbell, Theodore H. 1936. A Monographic Revision of the Genus *Ceuthophilus* (Orthoptera, Gryllacrididae, Rhaphidophorinae). *Biol. Sci. Ser., Univ. Florida* 2 (1): 551 pp. 38 plates. \$3.75.

thousand specimens were examined in the preparation of the revision. The systematic treatment of the species is, of course, beyond critical appraisal at present but impresses one as a model of taxonomic work.

In addition to notes throughout the text on the habitats of the various species the author has added a summary of what is known of the ecology of these insects including food habits, predators and social and commensal relations. The paper closes with a short, interesting speculation on the phylogenetic history of the genus, which attempts to indicate the geological and ecological features which have contributed to the origin of the subgeneric groups and species. Hubbell's observation is that the more primitive species are the most widespread; the more specialized types occur on the periphery or are segregated within the range of the supposedly ancestral type, a phenomenon with which "Matthew's Law" is not in accord. Three primary centers of evolution are postulated: the Eastern Deciduous Forest Region, the Sonoran Region and the Northern Great Basin.

Twelve of the thirty-eighth plates are maps showing the geographic distribution of the species considered in groups; the other plates depict diagnostic characters of the various species.

Those interested in Orthoptera will look with eagerness to further publications promised by the author on this group of insects.

H. F. STROHECKER

UNIVERSITY OF CHICAGO

VEGETATION OF NORTHERN ALBERTA¹

Situated in northern Alberta, in the basins of the Peace, Slave and Little Buffalo Rivers, the Wood Buffalo Park is an area of some 17,000 square miles of nearly virgin wilderness. It is of low relief except at the southern edge where plateaux rise to 2000 feet. The surface is mostly morainic with large plains that apparently represent dry bottoms of postglacial lakes.

Raup spent considerable time in the Park from 1927 to 1930 and gives our first detailed botanical description of the area. It is largely covered with a forest of *Picea glauca* and *Pinus banksiana*, modified by fire in many parts and there *Populus tremuloides* and *P. tacamahacca* have appeared. Numerous muskegs or bogs are occupied by *Picea mariana* while other low areas are occupied by grasslands broken by willow scrub and aspen groves.

The flora includes 460 species which are listed with notes on their distribution, variations and frequencies. The various communities are presented diagrammatically with indications of their successional relations. A rather extensive literature is cited and the whole forms an important contribution to our knowledge to this region of northern coniferous forest.

GEO. D. FULLER

THE UNIVERSITY OF CHICAGO

¹ Raup, Hugh M. 1935. Biological investigations in Wood Buffalo Park. *Nat. Mus. Canada Bull.* 74: 1-174. 13 pl. 15 fig.

RELATIVE EFFICIENCY OF ROOTS AND TOPS OF PLANTS IN PROTECTING THE SOIL FROM EROSION ¹

Plant cover provides the chief protection of the soil from erosion. Agronomists, ecologists, engineers, and others working on the problems of soil conservation are directly concerned with the relative efficiency of different plants in withstanding erosion. This bulletin contains information on this subject for a number of the more important field and garden crops, weeds, shrubs, and grasses. Samples of the soil in which the plants were growing were obtained from fields, pastures and prairies by placing a wooden frame 1 × 0.5 meters tightly about a representative small plot of the crop and soil to be tested. The core of the soil was cut away to a depth of 1 dm. and a tight bottom attached to the frame without disturbing the soil structure or plant cover. The samples, taken in pairs, were transferred to a rack which sloped at an angle of 10°, and the relative time required to wash away the soil was determined with the plant cover intact and the cover clipped to the soil surface and removed. A stream of 13 gallons of water per minute from an open hose was played uniformly over the sample at a height of 2.5 feet and under a total force of approximately one pound per square inch. All living underground parts were recovered and dry weight determined separately from that of the tops.

Bare soil, consolidated by occasional watering during four weeks, eroded in 16 to 18 minutes. The roots alone of 30-day old sunflowers, millet and Sudan grass each resisted erosion two to four hours. With tops also intact 35 or more per cent of the soil was left after 9 to 12 hours of watering.

Turkey red winter wheat planted on lowland soil eroded in 7 to 11 minutes in the late fall and early spring with the tops removed and 11 to 19 minutes with the tops intact. As the crop developed, the roots alone more than doubled in efficiency in resisting erosion while the protection afforded by the maturing tops increased nine to ten fold. The protection reached the maximum when the grain was in the early dough stage and decreased rapidly at ripening and after harvest. Oats was similar to wheat but less efficient in retarding erosion. It was shown that resistance to erosion does not result so much from a cover of great vertical thickness as from one widely spread and continuous.

Fall seeded alfalfa on upland soil eroded the following April, required 7 minutes without and 8 minutes with the tops to completely remove the soil. As the plants matured their resistance was moderately increased, requiring 18 minutes without and 48 minutes with tops by the latter part of the following October. Four year old alfalfa plants 28 inches tall from lowland soil required 43 minutes with and 21 minutes without the tops for complete erosion.

¹ **Kramer, Joseph and J. E. Weaver.** 1935. Relative efficiency of roots and tops of plants in protecting the soil from erosion. *Conservation and Survey Division, Univ. of Nebraska Bull.* 12. 94 p., 37 fig., 17 tables.

The root systems of corn and sorgo were inefficient in retarding erosion. Their leaves when grown in closely spaced rows afforded much protection by breaking the force of the water.

Sudan grass was found to be more efficient in retarding erosion than any of the field crops investigated. The efficiency was greatly increased as the crop matured, the long leaves and strong, fibrous root system being the major factor in its efficiency. Biennial sweet clover and rape afforded good resistance to soil erosion when closely seeded and with the tops remaining on the plants.

All the garden crops afforded little protection from erosion, without the tops. Tomatoes afforded the greatest protection, the bushy tops delaying erosion for one hour and six minutes. Without tops the soil held only 13 minutes.

Weeds in general were only fairly effective in holding the soil. Their efficiency depended largely upon the amount and density of the top growth.

Of the cultivated pasture grasses Hungarian brome grass afforded the greatest resistance to erosion. Two hours and 25 minutes were required to erode the soil when the tops were removed and about twice as long with the tops intact. Blue grass was a little less efficient, and big bluestem required a much longer time than brome grass. Slough grass was the most resistant to soil washing of any of the grasses tested. This is due mainly to its heavy foliage.

The bulletin contains data on the comparative dry weights of living underground plant parts in the surface four inches, of all the plants tested. It is well illustrated, containing very good diagrammatic drawings of the root systems of most of the plants. Graphs are effectively used to show the efficiency of crop plants in withstanding erosion with and without the tops. The bulletin is well prepared and should prove of much value to all workers in Soil Conservation. The methods that were developed should also be valuable in obtaining information in a very short time on the relative efficiency of all plant cover under different soil and climatic conditions.

A. E. ALDOUS

KANSAS STATE COLLEGE OF AGRICULTURE,
MANHATTAN, KANSAS

EVOLUTION AND SPECIATION ¹

Professor Shull has broken away from the standard presentation of evolution in this book and properly places the emphasis upon the origin of species. Although the book is designed as a text for college classes, no other book has brought the essentials of the process of speciation together in a balanced treatment. The work is readable and flavored with personal comments and opinions.

¹ Shull, A. F. 1936. *Evolution*. 312 pp. 64 figs. McGraw-Hill Book Co., New York. \$3.00.

Naturally the genetic aspects of evolution receive special attention and recent activity among the geneticists has resulted in great strides toward the solution of the old problem of species origin. After reviewing the advances made in this field, it is difficult to believe that Bateson stated in 1921 that little was known concerning the origin of species. It would seem that we now are able to recognize all of the essential principles of evolution, even though there yet remain masses of facts to be discovered and the play of factors to be interpreted for each species.

The school of naturalists who so ably organized their observations into the concept of evolution are represented today by the ecologists and taxonomists. Ecology, in the process of becoming experimental and physiological, has tended more to the description of communities and the mechanisms of interaction between the organism and its environment. As in the case of the physiologist, the modern ecologist seldom seems to ask himself the evolutionary origin of the interaction he observes. This tendency to avoid the problems of evolution is more astonishing considering the fact that natural selection was the heart of the Darwinian theory and natural selection is surely a great principle of ecology.

Not only should ecologists be in the lead in the modern investigation of the process of natural selection, but another highly important factor in evolution, that of isolation, commonly has an ecological basis. The ecologist with a penetrating mind must inquire into the origin of the units of the community and the nature of the processes which resulted in the adjustments of organisms to their environment. The ecologist can make great contributions to the solution of the problem of evolution, but at the moment we must admit that the major activity emanates from the students of heredity.

In view of the overemphasis that Darwin places upon adaptation and the later swing away from adaptive interpretation, Professor Shull strikes a fine balance. He is possibly inclined to emphasize nonadaptiveness a bit more than is warranted by the facts. This tendency culminates in a general attack on the concept of mimicry which seems to the reviewer to be the weakest part of the book. Although Professor Shull overlooks many well known facts which support the concept of mimicry, much of the blame for his point of view can be laid at the door of the ecologists who have failed to test the concept with rigid experimentation and who too often include fanciful examples of supposed mimics beside the examples which will bear critical scrutiny. Professor Shull's treatment of the concept of protective coloration indicates that he can be convinced through direct experimental attack but that statistical evidence of correlation does not carry the same weight.

Mimicry, however, is merely a case, and it cannot be said that Professor Shull lacks an appreciation of the problem of adaptation in general nor that he overemphasizes natural selection as a factor of evolution. Taken as a whole, the reviewer believes this book to be an excellent and balanced treatise on

modern evolutionary problems well adapted to the college student and thought provoking for the investigator in this great field of biology.

ALFRED E. EMERSON

UNIVERSITY OF CHICAGO

RUNOFF AND EROSION IN RELATION TO GRASSLAND VEGETATION

The influence of grassland vegetation upon surface runoff and soil erosion has not received the attention it merits. This subject is of particular interest and importance in regions where natural forest cover is scanty or lacking. Consequently, the recent paper by Weaver and Noll¹ setting forth their investigations during the period 1933 to 1935 is most welcome.

The authors adopted the so-called "runoff-plot" method utilizing enclosed plots 3 feet wide and 33.3 feet long. Natural rainfall was supplemented by artificial watering when this appeared desirable. During a 15 month period with 26.88 inches of rainfall, runoff on a 10 per cent slope amounted to 2.5 per cent from prairie, 9.1 per cent from over-grazed pasture, and 15.1 per cent from a pasture the soil of which had been bared by excessive grazing. The amount of soil eroded from prairie was not measurable and from the pasture the amount was very small; loss from the bare area, however, amounted to 5.08 tons per acre. Although this is merely a sample of the data presented, it may serve to indicate the qualitative relations established.

The conclusion was reached that where there is a good cover of grass on the ground there is no serious problem of erosion. "A soil covered with its natural mantle of climax vegetation represents conditions most favorable to maximum erosion control."

The use of vegetation in soil erosion control work is now a technique which is generally accepted as desirable. Forest tree species and other woody plants suitable for planting on areas subject to erosion have been investigated by many workers and in numerous cases their value proven beyond doubt. However, we must not overlook or minimize the high efficiency of grasses in erosion control. The increased use of grasses, especially native grasses, is greatly to be desired. Trees and other woody plants do not have a monopoly in the control of surface runoff and soil erosion.

H. J. LUTZ

YALE UNIVERSITY SCHOOL OF FORESTRY

¹ Weaver, J. E., and Wm. C. Noll. 1935. Comparison of runoff and erosion in prairie, pasture, and cultivated land. *Conserv. Dept., Conserv. and Survey Div., Univ. Nebraska. Bull. 11.* 37 pp. 11 figs.

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NOTES AND COMMENT

A PLANT SOCIOLOGICAL HERBARIUM BASED ON SYNUSIAE¹

In connection with the summer course in plant sociology at the Biological Laboratory, Cold Spring Harbor, Long Island, the author has started a plant sociological herbarium based on the synusiae. A synusia is "a natural community of species belonging to the same life-form groups and with uniform ecological requirements."

Rübel² has emphasized the importance of synusiae in the field of community description. He says, "In the ecological description of an association one must seize upon these synusiae. They are in several cases in accord with the layers but not always, as, for example, in the epiphytic communities on bark." Tansley and Chipp³ say, "It is clear that the structure of any of the ordinary complex communities . . . can be analyzed into synusiae. . . . Such analysis gives a deeper insight into the constitution of a community." Warming and others early recognized the numerous life-form groups composing the more complicated types of vegetation, such as forest complexes. Lippmaa has recently published on the vegetation of Esthonia using the synusiae as the basis of his classification of the communities and elevating them to the rank of associations. His one-layered association theory, however, is not meeting with a wide acceptance⁴ and was disapproved by the International Botanical Congress, Amsterdam, 1935.

It is not intended at this time to discuss the merits of the one-layered association theory but to describe the method of herbarium organization at The Biological Laboratory.

In the plant sociological herbarium the synusia constitutes the smallest unit. Herbarium specimens of each species in a particular synusia are grouped together in one folder. The folders representing the synusiae of a phytocoenosis, or complex community, are grouped together in the herbarium into a subsection. On completion of the herbarium there will be as many subsections as there are vegetational types (phytocoenoses) and each subsection will consist of one or more folders according to the number of synusiae composing the phytocoenosis. Together with the folders for the synusiae of a phytocoenosis is one containing the sociological data derived from a study of the various stands of that type. This herbarium organization can be illustrated by the following list of folders in the subsection concerning the forest type (phytocoenosis) dominated by *Acer carolinianum* of the tree layer.

Folder No. 1 contains sociological data from the various stands of the *Acer carolinianum* association studied, and includes: (a) tables of quantitative data (frequency, coverage, basal area, constance, etc.) derived from quadrat analyses of the constituent synusiae; (b) tables of qualitative data (life-form, sociability, periodicity, dynamogenetic role, etc.) derived from notes concerning the plants of the communities studied; (c) lists of species, when quadrat studies are not made; (d) diagrams, charts, etc.; and (e) climatic and edaphic data concerning the synusiae, or phytocoenosis as a whole.

Folder No. 2 contains herbarium specimens of the species of the arborescent synusia which is dominated by *Acer carolinianum*.

¹ Contributions from the Botanical Laboratory, The University of Tennessee, N. Ser. 8.

² Rübel, E. 1930. Pflanzengesellschaften der Erde. Bern.

³ Tansley, A. G., and T. F. Chipp. 1926. Aims and methods in the study of vegetation. London.

⁴ See page 444 of this issue and Cain, S. A. 1936. Amer. Midl. Nat. 17 (3).

Folder No. 3 contains herbarium specimens of the species of the frutescent synusia dominated by *Clethra alnifolia*.

Folder No. 4 contains specimens of all species of the herbaceous synusiae usually dominated by *Osmunda cinnamomea* and *Spathyema foetida*.

Folder No. 5 contains specimens of species of the aquatic synusiae of the small streams along the banks of which the forest type is found.

Folder No. 6 contains packets of plants of the species of the cryptogamic synusiae. These packets are grouped according to the substrata occupied by the plants, i.e. mosses, liverworts and lichens of bark, of the peaty shrub stools, etc.

Folder No. 7 contains herbarium sheets of species of a dominant frutescent community which is apparently ecotonal to the Aceretum of the streamside and the Pinetum of the adjacent upland. This one-layered community, called by Conard,⁵ "low-shrub association" is closely related to but not identical with the frutescent synusia of the Aceretum.

The above treatment of the Aceretum carolinianae is representative of the subsections of the herbarium. In a like manner, other forest phytocoenoses such as the Pinetum rigidae and Quercetum montanae are represented by subsections and separate folders for the synusiae. The various subsections of the herbarium are arranged in sections according to their physiographic relations. Thus, the Aceretum carolinianae belongs to the outwash plains of the pine barrens region, the Quercetum montanae to the morainal region of the north shore, etc.

The subsections within a section are arranged in a sequence according to their floristic relationships, determined largely on a basis of the dominants of the superior synusiae.

Much can be said for the practical aspects of such an herbarium in connection with class work and research in plant sociology. First, the smallest units in the herbarium, the folders, correspond to the smallest natural units of vegetation, the synusiae. These are the most practical units with which to work in detailed sociological and instrumental field study. Second, the grouping of synusial folders into subsections on a basis of phytocoenoses allows the ready consideration of the vegetation represented on a basis of the prevailing several-layered association concept. Third, the sections of the herbarium represent a classification of the vegetation on a physiographic basis (a scheme widely used in America). This seems to be a practical arrangement for the vegetation of Long Island. Fourth, within the various vegetational complexes certain successional relationships can be illustrated by the sequence of subsections in the herbarium, without, however, placing too great an emphasis on the dynamic aspects of the vegetation and on the monoclinal theory. Fifth, as the herbarium approaches completion the problem of identification is simplified for the student as he can determine his collections from a particular association by reference to the appropriate folders in the herbarium. As taxonomy is not the goal but the tool of the plant sociologist this is a valuable adjunct. Sixth, for any circumscribed region the herbarium would never become very bulky. No matter how many stands of any one synusia are studied in the field work each species of the synusia does not need to be represented in the herbarium more than once. The presence, or constance, of the species can be ascertained from the tabular data in the first folder of each subsection.

Another basis for the arrangement of the synusial folders would be the formation in the most widely used modern sense, i.e. community groups of similar life-form, but not necessarily, in fact frequently not, closely related floristically. The arrangement according to formations can be either on a basis of the life-form of the dominant synusiae, treating the entire phytocoenosis as a unit, or on a stricter life-form basis grouping together the folders of mesophanerophytic, microphanerophytic, nanophanerophytic, geophytic synusiae, etc.

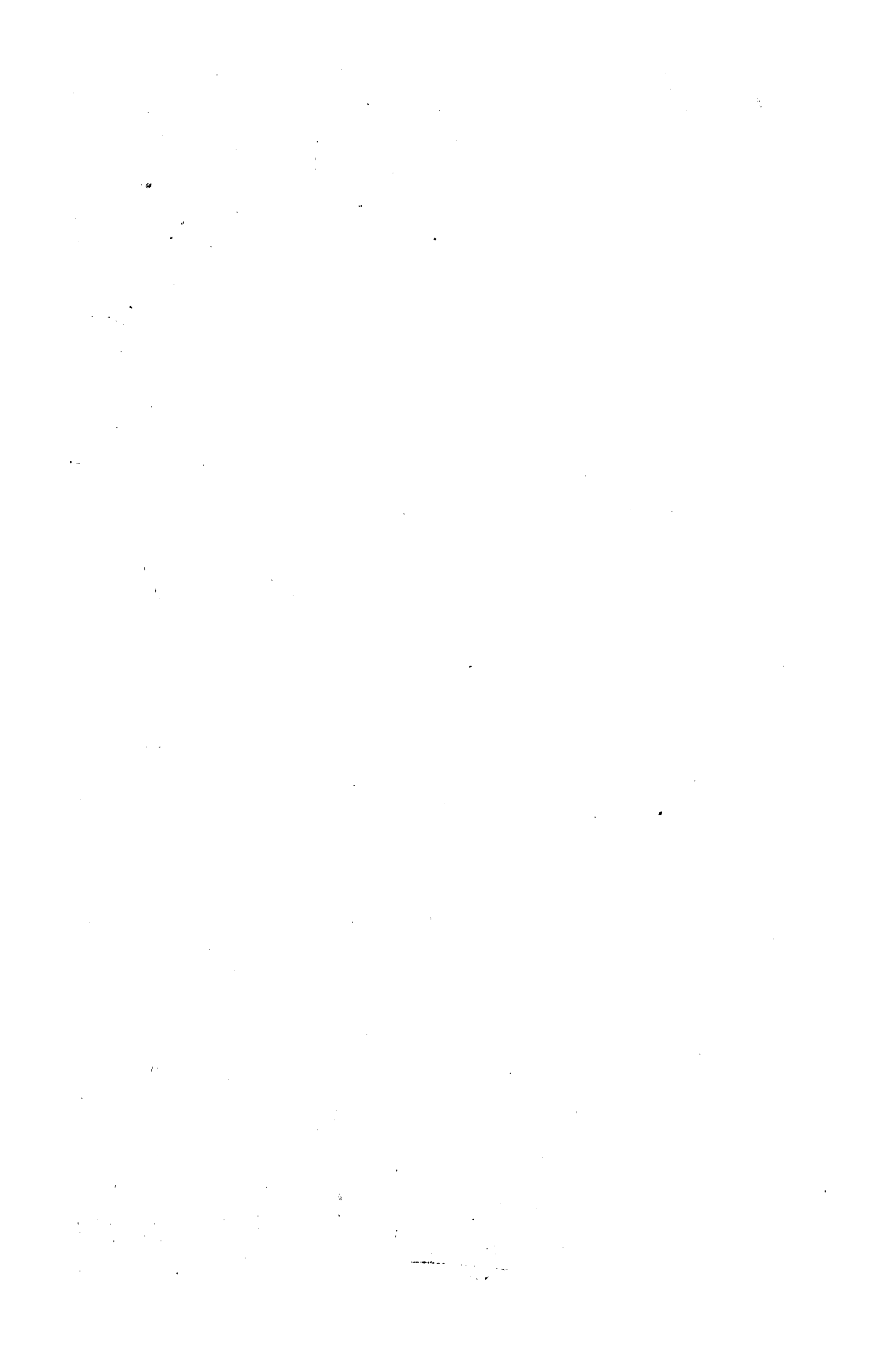
⁵ Amer. Midland Nat. 16 (4): 433-516. 1935.

Still another scheme for the arrangement of the synusial folders would be strictly on a basis of floristic composition of the synusiae, placing together those synusiae which form natural alliances, orders, etc., the whole following the sequence of sociological progression.

In so far as the author has been able to ascertain, nowhere else is such an herbarium being made. Such an herbarium is recommended for local, intensive work in plant sociology because of its practical aspects, not the least of which is its plasticity and the ease with which it lends itself to interpretation of the vegetation represented on a basis on any of the existing points of view. The secret of this lies in the use of the synusiae as the fundamental unit. Preparation of such an herbarium is not recommended for extensive regions.

STANLEY A. CAIN

THE UNIVERSITY OF TENNESSEE,
KNOXVILLE, TENNESSEE



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GROWTH BEHAVIOR IN *CONVOLVULUS SOLDANELLA* L.¹

EDITH A. PURER

San Diego, California

During a period of nearly three years the growth behavior of *Convolvulus soldanella* L., the beach morning-glory, was observed monthly. The plant, growing along sandy sea-beaches, is a herbaceous perennial with a much developed, branching rhizome system. The specimens used in this investigation grow on a sandy spit which extends from Coronado to North Island, San Diego County, California.

In general, at about ten centimeters below the surface, the *Convolvulus* has numerous, branching, whitish, fleshy rhizomes. From the lateral, and sometimes from the terminal buds, there arise short, thin, reddish aerial branches each bearing four or five leaves. Occasionally in the early summer, these aerial branches grow to three feet or more in length, dying at the end of the summer season. In addition to the usual growth development of this plant, there were in the spring of the year interesting aerial arches, produced by the tips of the rhizomes rising above the surface of the sand, and, as they continue to grow, burying themselves to their former level. It was this phenomenon which prompted a study of the growth behavior of the plant.

PHYSICAL CONDITIONS

Precipitation data obtained from the United States Weather Bureau station at San Diego, about three miles from the locality of experimentation, show that the rainy period extends from September or October to May (fig. 1). Monthly maximum and minimum air temperatures indicate that there is a gradual rise during the summer, and a gradual lowering in the winter months, the total yearly range being small. The area is frost-free.

The sand spit is exposed to winds from all directions, especially to the prevailing winds which sweep across it from the ocean. With such a lack of protection from the wind and with rather intense light, one would assume

¹ Presented before the Ecological Society of America at its meeting on June 28, 1935, at the University of California at Los Angeles.

that evaporation rates from both black and white Livingston atmometers, which had been set out for a portion of the period of the investigation, would be high. However, the presence of both low and high fogs results in some degree of modulation and causes rather low evaporation rates.

During a part of this period soil moisture samples were taken at a depth of 10 to 30 cm., the approximate depths at which roots are found. Ranges in soil temperature are to be found in table I.

TABLE I. *Range of soil moisture, in percentages of dry weight. The sand has a wilting coefficient of 1.5%*

	Depth in cm.		
	10	20	30
September, 1932	.4	.5	.6
October	1.4	3.9	2.6
November	2.6	3.1	3.6
December	2.1	3.2	3.0
January, 1933	5.0	5.7	5.8
February	2.7	3.9	3.5
March	2.0	3.1	3.1
April	.5	1.4	3.0
May	.6	3.6	3.4
June	.6	1.7	2.1
July	.5	.7	1.3
August	.4	.6	.6
September	.3	.5	.6
October	.2	.2	.3
November	.3	1.2	2.9

The soil is loose, incoherent, rather coarse sand, containing about ninety per cent of quartz, a little feldspar, with basaltic material especially prominent.² This soil is poor in nutrient materials, since organic substances which may be left in the soil are rapidly decomposed, and, owing to the physical structure of sand, the rainwater carries the humus particles deep into the soil (Purer, '36).

Soil temperatures were taken weekly during a portion of this period by means of maximum and minimum thermometers placed horizontally at a depth of 30 cm. in wooden boxes, so constructed as to prevent circulation of air, while at the same time permitting ready access to the instruments. From table II it may be seen that the maximum soil temperature during the week of August 10 to 16, 1933, was 82° F., and the minimum, from January 25 to February 8, 1933, was 50° F. The highest weekly range was 12° F., the lowest 0° F. The temperatures in the soil are not subject to much fluctuation (table II).

² Soil analysis was obtained through the courtesy of the U. S. Bureau of Chemistry and Soils.

TABLE II. *Weekly soil temperatures*

	Max.	Min.		Max.	Min.
1932			1933		
Sept. 6	74	71	April 5	68	57
13	74	69	12	70	59
20	71	69	19	72	61
27	70.5	68.5	26	71	63
Oct. 4	70	68	May 3	69.5	61
11	71	66	10	69	62
18	67	65	17	69.5	60
25	68	64	24	70	62
			31	70	64
Nov. 1	67	64	June 7	70	64
8	66	62.5	14	70	66
15	66	62	21	72	67
22	66	63	28	73	67
29	65	62			
Dec. 6	64	59	July 5	73.5	68
13	62	53	12	73	69
20	58	52	19	75	69
27	62	52.5	26	76	73
1933			Aug. 2	76	76
Jan. 4	59	52	9	77	71
11	57	53	16	82	72
18	58	51	23	80	71
25	59	50	30	78	70
Feb. 1	57	50	Sept. 6	77	68
8	56	50	13	76	68
15	57	53	20	79	67
22	59	52	27	78	67
Mar. 1	61	52	Oct. 4	77	68
8	63	53	11	77	68
15	62	54	18	75	67
22	64	56	25	76	67
29	65	54			

EXPERIMENTAL STUDY

In order to secure rates of linear migration, twenty-five fleshy-tipped rhizomes were metal-tagged and the growth recorded monthly. In addition, at certain periods during each year, rhizomes were marked off with India ink at even intervals to determine the exact place of elongation.

Rhizomes were placed in wooden boxes twenty-four inches long, four inches wide and four inches high, open at each end. These boxes, with or without a layer of sand inside, were buried at varying depths. In addition, other rhizomes were buried at different depths, some underneath boards, some were placed above boards buried in the sand; while others were raised to or above the surface of the sand. Additional water was supplied to some rhizomes to augment the amount received from rain. High storm waves covered some with salt water. These various methods were used to ascertain the reactions of the rhizomes to habitat conditions.

During certain periods of the year the rhizomes exhibited an interesting phenomenon. The rhizome would rise to the surface, form an arch, and descend to its usual level in the soil. Many rhizomes were tagged, marked, and their growth measured to determine, if possible, the cause of such behavior.

GROWTH OF THE RHIZOMES

Growth is continuous throughout the year, the maximum period being from March to July, that is to say, toward the end and after the expiration of the rainy season at which time there is a rise in temperature. Some growth of the rhizome precedes the appearance of aerial leafy shoots. As the temperature continues to rise, and during the period of maximum temperature, growth is slow. The minimum period of growth is during the coldest portion of the year, the time when the heaviest rains occur (fig. 1).

The elongating region of the rhizome is at the extreme growing tip. The extent of its growth in length in the ground is enormous as compared with that which takes place when it rises to the surface and becomes an aerial branch.

The rhizomes of the terminal ends are whitish and about twice as thick as those produced by lateral buds, but when terminal ones are injured, or when they rise to the surface and subsequently die, the lateral buds nearest to them grow and produce a thicker and whiter rhizome. Rhizomes below the surface are succulent, white to pinkish when young, but turn tan or brown when older. When they grow above the surface, they become red and decrease in diameter. The rhizome tip may be very succulent, but as it grows it may become narrow and half as fleshy. With new growth it again becomes as wide and as fleshy as the rest of the rhizome.

CAUSES INFLUENCING BEHAVIOR OF RHIZOMES

Actively developing rhizomes are found about 10 cm. below the surface of the sand. Older rhizomes may be buried more deeply, as the sand washed up by the waves is dried and later blown inland by the wind and deposited around the plants. All old rhizomes produced during previous seasons are from 2 to 15 cm. below the present season's growth since the level of the sand varies with storms and with the intensity of the wind, but as the vegetation during the spring and early summer aids in stabilizing the sand, little movement takes place during these periods.

When rhizomes are covered by sand, the growing tips tend to regain their previous level; when a small quantity of sand is removed, the tips tend to revert to their usual level. When artificially changed from their horizontal position to a sharply vertical one, they have a tendency to curve sharply back to their previous level, forming an arch in the ground. The arch may vary from 3 to 15 cm. in height.

The releasing of pressure, by placing of a rhizome at its natural level in a box instead of in the sand, changes the thick, fleshy white rhizome to a red, thin, less fleshy aerial shoot. Again, when the rhizomes placed in boxes become aerial shoots, they turn in the narrow box to the nearest end, growing to the surface and developing several leaves. Aerial shoots buried in the sand or placed below boards or in sunken boxes invariably die. However, with the death of the terminal shoot, the lateral buds farther back grow into rhizomes. The rhizomes in a deeply buried box were found without exception under the upper side of the box, while those which had been placed in a box near the surface lay on the bottom of the box. Some of these buried rhizomes died, as a result, probably, of having been buried too deeply, or because of lack of moisture in the box.

Temperature is probably one of the most important factors which influences the rhizome growth of *Convolvulus*, since increase in growth does not occur until there is a rise in temperature. In March, 1935, an unusually cold month, growth of all parts of the plant was retarded, as compared with March records in 1933 and 1934 (fig. 1). Too high a temperature during the summer probably acts as a restraining agent. There is, of course, less variation in the soil temperatures than in air temperatures. Temperature change apparently has no relation to the height or the depth at which the rhizome grows in the ground.

When there is a maximum amount of rain, there is the least amount of growth. This seems to be due not to the abundance of precipitation but rather to the low temperatures. While the soil, due to its porous nature, is never saturated with water, roots of most plants are found in a moist layer, the upper dry layer acting as a mulch.

The difference of level cannot be due to moisture relations, entirely, if at all, because the winter level, when most moisture is present, and the late summer level, when moisture is at the minimum, do not differ. The watering of plants produced no effect upon their level.

Wind plays an indirect part when it attains high velocity and transports sand from the water's edge and deposits it around the *Convolvulus* plants. The rhizome then ascends until the usual level in the sand is reached. The wind has no effect on the length of growth of the rhizome. It does aid in increasing evaporation rates, but atmometer readings during a portion of the period fail to show any correlation with the growth of the rhizome.

Light appears to have no effect upon the growth of the rhizome, other than its probable importance in warming the sand, for the number of days of sunlight has no effect upon the rhizome's relative length of growth.

The passage of the rhizome through the porous sand is easily affected. The sand being of the same quality throughout, the pressure exerted by it is uniform. If, however, the rhizome be placed deeply in the sand, or if it be buried more deeply by the wind blowing sand over it, it will regain its previous level.

Contraction of the roots has been regarded as the means of keeping many rhizomes at their level. While this may be true of some types of rhizomes, examination shows that roots do not generally appear at the end of the rhizome. In fact, the first indications of roots, too small to exert a contraction and resulting pull on the rhizome, are to be found from 20 to 50 cm. behind the tip. Moreover, while experimenting with the tip, it is easy to cause it to rise or lower its level, without roots being present to cause any contraction.

Fuller ('31) states that "Experiments on *Polygonatum* show that the distance separating the rhizome from the place where the aerial shoot emerges into the light is the chief depth-determining factor." However, in the case of *Convolvulus* rhizomes, the level of the growing tips changes in the ground although no aerial branches be present at the actively growing tip, or nearer than 20 to 50 cm. away from it.

Variations in level of rhizomes of other plants may be due to differences in the oxygen content of the soil, but where the oxygen supply is as abundant as it is in a sandy soil, this would not be a determining factor.

FORMATION OF ARCHES

The first appearance of arches was in February of 1933 and 1934 and in March of 1935. New arches continued to be formed during the period from February to June. Each month some were found to be dead. All disappeared or were found dead after September or October, and none were in evidence until the following February. During the season of September, 1934, to February, 1935, all aerial arches had died, but during excavation several small arches appeared to be living. It is possible they might have been on the surface earlier in the season and later were covered by sand.

There is considerable variation in their height and length. An average of all measured arches gives 15.4 cm. as the width of the arch at the surface of the ground and 7.2 cm. as its height above the surface. There are about 35 cm. lost in linear migration in the formation of arches (fig. 2).

Rhizomes, after coming to the surface and arching, return to the ground at about the same level. Usually, after developing an arch, they continue to grow in the same general direction. This happens in the large majority of cases. However, excavations have shown that there are a number of deviations from this general rule. The rhizome may take the opposite direction in several different ways (fig. 3). This is not due to competition for space, as no rhizomes or roots of other plants are present. Two arches may form on the same rhizome in the same month. Arches are usually without leaves, but occasionally small leaves, and, very seldom a short branch, 2 to 5 cm. long, may develop. Buds are usually present.

The thickness of the arch varies. It is usually of the same thickness as the fleshy rhizome, but about one-fifteenth of all arches measured were found to be thinner than the rhizomes from which they developed.

No rhizomes could be forced to arch either in the air or in a box. Arches could always be forced under the surface by changing the position of the growing tip from its level in the sand to a lower level. It then grew to its

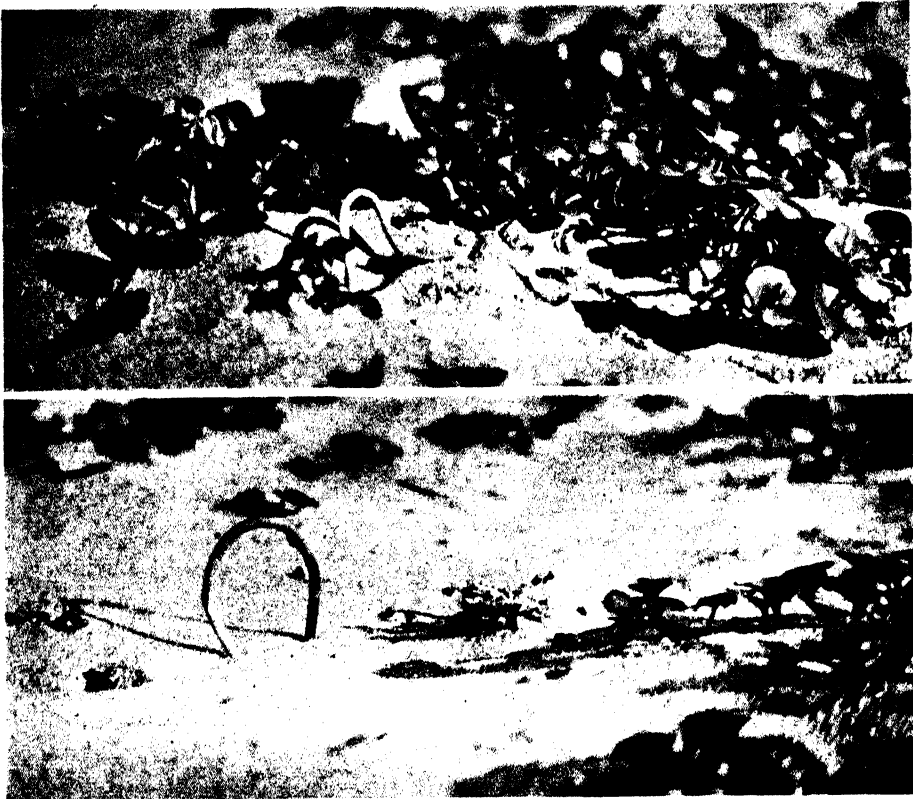


FIG. 2. Above: *Convolvulus* with arch and many prostrate aerial shoots, one having a flower. Below: Arch formed from rhizome. Note at the left the pure white growing tip.

usual level, forming a small arch. Rhizomes with tips raised to the surface or pointing into the air either died or grew down to their previous level.

Most arches were formed from terminal buds, but often from lateral buds,



FIG. 3. Diagrams illustrating the arch development. At left, the usual formation; at right other directions of growth. The horizontal line represents the surface of the sand.

such being the case when the terminal bud had come to the surface and had died. Occasionally, red lateral branches arch, the growing tips then bury themselves and later come to the surface with a branch development of five or six leaves. Whenever growing tips from the red lateral arches stayed

buried, they continued their growth as white, fleshy tips. Arches once formed never grow larger. Growth is at the tip of the rhizome. One rhizome, after forming an arch, grew 119 cm. in five months, a remarkably rapid rate.

There are three methods by which the rhizome reaches the surface: (1) (most common) short aerial stems (usually from the lateral buds) come to the surface and flower. These die in autumn; (2) rhizomes (usually the terminal ones) come to the surface, arch, and return to their level in the sand. Buds, which sometimes develop leaves, form on an arch. No flowers were in evidence at any time on an arch; and (3) short aerial stems (mentioned in no. 1) develop long prostrate surface stems, with numerous leaves. These die at the termination of the growing season.

WHAT CAUSES THE ARCHES TO FORM?

When rhizomes had the pressure of sand removed above them, they did not arch but grew down to their former level. Those with their growing tips forced to the surface either died or returned to their previous level and did not form arches. When its forward growth was blocked by a heavy piece of wood, the rhizome did not arch but turned either to the right or to the left. Rhizomes in wooden boxes, where the pressure of the sand had been released and yet where there was moisture and darkness, lost their fleshy appearance and developed leaves, but formed no arches. If buried at its usual depth in a box of moist sand, the rhizome kept fleshy and grew through the box and into the sand outside the box. One such rhizome grew 78 cm. from one entrance of the box and through the box to the sand outside where it developed six lateral branches. If buried deeper in the box than their normal depth, the rhizomes grew along the under side of the top of the box, otherwise they lay on the bottom. Rhizomes, buried under boards at a depth of 20 cm. in the sand, died. When aerial shoots with well-developed leaves were placed under boards, they died, with the exception of one in which the tip grew 4.3 cm. past the board and came to the surface; and another instance two tips grew to the surface between cracks in the board. To summarize, pressure causes differences in levels of rhizomes but has no apparent influence on the formation of arches.

Arches form during the period when there is an increase in the number of days of sunshine, but since the rhizomes are located in the soil, light may affect such development only because radiant light is changed into heat. Arches form after the period of greatest precipitation when temperatures are gradually rising.

Goebel ('05) states of *Polygonatum* that the means which this plant adopts to bring its shoots into the soil or above it are evidently governed in the first place by changes in its geotropic sensitiveness, and this itself is most probably conditioned by processes of metabolism. In *Convolvulus* the rhizome, being geotropic, seems to become, during certain conditions in which

there is a rise in temperature and sufficient moisture, phototropic and rises to the surface. Later, conditions change and it becomes geotropic, growing down to its old level.

SUMMARY

1. *Convolvulus* spreads by means of rhizomes about 10 cm. below the surface of the sand. In addition, it forms short aerial branches, and, during summer, long prostrate aerial branches. During a portion of the year the rhizomes produce aerial arches. The rhizomes in the soil are whitish, thick, and succulent; when these arch into the air, they remain thick and fleshy, but when they rise to the surface and form aerial branches, they turn reddish and become thin.

2. Growth in the rhizome is continuous throughout the year, the greatest amount occurring from March until July, following the maximum amount of rain and before the maximum temperatures are reached.

3. Rhizomes maintain their level in the soil, and, despite change by wind or human agency, they return to their level at their growing portions, although some shoots near the surface may become aerial. When pressure is released, however, as when the rhizome is inserted into a buried box, the rhizome turns into an aerial shoot.

4. Growth is at the extreme tip; arches form at the tip and not from any portion of the rhizome behind the tip. Neither do they form in consequence of any backward motion of the tip, as the resistance of the sand would thus be much greater than would result from pushing forward a single tip.

5. The first appearance of arches is in February or March. With the increase in the growth of rhizomes during the early summer, the arches increase in number. In August no new ones develop, and by September most of them are dead.

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ECOLOGICAL OBSERVATIONS ON SPAWNING AND EARLY
LARVAL DEVELOPMENT IN THE OLYMPIA OYSTER
(*OSTREA LURIDA*)¹

A. E. HOPKINS

U. S. Bureau of Fisheries

The native oyster of the Pacific coast is biologically different, in some respects, from the common Atlantic coast species (*O. virginica*). Like the European oyster (*O. edulis*) it is hermaphroditic as well as viviparous, as described by Stafford ('13, '14). More recently Coe ('31a, '31b) investigated the species and found it to be clearly protandric. He described spermatogenesis in detail and demonstrated that throughout the life of each individual there is an alternation of male and female phases, although in either phase the germ cells of the opposite sex may be found.

The process of spawning was well described by Stafford ('14). He stated that eggs are discharged into the branchial chamber in which they are held as in a brood sac. Spermatozoa, on the other hand, are discharged directly into the surrounding water. At this time they are in clusters, or sperm balls, from which the individual sperms escape when brought into contact with seawater, according to Coe ('31b), who estimated that each ball is made up of from 250 to 2,000 or more sperms. According to both Stafford and Coe the sperms are brought into the mantle chamber of functionally female specimens with the water pumped by the gills, resulting in fertilization. It is probable that the sperms stimulate spawning in this species, as was found by Galtsoff ('30a, '32) in other species of oysters, though this has not been demonstrated.

It is remarkable that although the oviducts of oysters open into the cloacal chamber the eggs are finally discharged from the mantle chamber, suggesting that they must pass through the ostia of the gills in a direction opposite to that of the normal flow of water. Stafford ('15), referring to *O. lurida*, described this activity as follows: "Eggs and sperms are liberated from the gonaducts into the suprabranchial chamber, and make their way through the water-tubes and gill-slits to the branchial chamber, which also serves as a brood chamber. In doing this they are assisted by the pressure of their mass. . . . Sections of oysters at the spawning season show eggs in the cavities of the gills. They do not pass readily through the gill-slits on account of the narrowness of the latter, but with increasing mass and pressure the gills become stretched and the slits enlarged, and besides the gills appear in places to suffer disintegration." Galtsoff (unpublished manuscript) made a recent study of the matter in *O.*

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virginica, and concluded that suction, due to opening of the valves during spawning, draws the eggs through the small spaces of the gills. That Stafford's and Galtsoff's observations apply to spawning by females is clear, as far as their explanations go, though the former considered sperms of *O. lurida* to be discharged in the same manner. While this may be correct, the writer has observed discharge of sperm balls directly from the cloaca, as in *O. virginica*.

Stafford ('14) estimated that in British Columbia waters the larvae develop for $16\frac{1}{2}$ days within the maternal brood chamber before they are released into the open water, where they develop for about 14 days more before becoming fixed. The total larval life would be about one month. Stafford's estimate, however, does not appear to have been based upon a complete analysis. Coe ('31b) stated the opinion that larvae develop in the brood chamber for "a period of approximately 10 to 12 days, perhaps." Larvae during this early period of development are found at the anterior end of the branchial chamber, adjacent to the labial palps and anterior ends of the gill lamellae. It is unknown by what mechanism they are kept in this place, from which silt and other rejected material are commonly swept out by way of the waste canal, a well defined band of ciliated epithelium of the mantle. The most thorough studies which have been made on this species were published by Stafford ('14, '15, '16, '17) in an excellent series of papers. His observations are frequently referred to in the following account.

NUMBER OF EGGS PRODUCED

There have been innumerable estimates of the number of eggs spawned by a single female oyster during a season. Galtsoff ('30b) reviewed the literature on the matter and indicated that previous estimates for average-sized females of *O. virginica* vary from about 9 millions to about 60 millions. He made what appears to be the most accurate counts of the number of eggs actually spawned. In a single spawning period the number of eggs discharged by the female of *O. virginica* varied from 15 millions to about 114 millions, and after the spawning had occurred the bodies of the specimens still contained a great number of eggs. During three spawning periods a specimen of *O. gigas* discharged a total of about 92 million eggs.

However, these species are of the oviparous type which discharge the eggs directly into the surrounding water, and they are in general many times larger than the viviparous species such as *O. edulis*, *O. equestris* (Gutsell, '26), and *O. lurida*. In the latter, in which the larvae develop for some time within the branchial chamber, one would hardly expect such tremendous fecundity. Moebius ('83), using an apparently accurate method, concluded that the average brood of a full grown specimen of *O. edulis* consists of about one million larvae. Individuals of the species, *O. lurida*, however, are much smaller, and Stafford ('18) estimated the brood at about one million larvae.

In order to obtain more accurate information on the spawning of this species, counts of larvae in single broods were made by the dilution method, by means of a standard counting plate. A specimen was carefully opened and rinsed thoroughly in seawater to insure removal of all larvae from the gills and mantle. Formaldehyde was then added to immobilize the larvae. The quantity of water in which the larvae were immersed was carefully measured and shaken to insure accuracy. Many of the adult specimens were of the size which would reach market during the following season, though some of them were quite small. In one series (table I) the broods of larvae from 13 speci-

TABLE I. *Number of larvae in broods produced by specimens of different sizes*

Specimen No.	Length (m.m.)	Width (m.m.)	No. of Larvae
121	32.7	23.5	130,628
125	30.3	24.0	113,142
126	28.0	23.5	95,667
127	29.5	27.5	150,600
128	29.0	23.0	156,875
129	29.7	21.2	184,114
130	31.0	25.8	355,500
131	23.5	19.2	69,490
132	28.2	24.4	126,174
139	36.2	26.3	293,473
140	29.2	27.0	213,781
141	28.5	23.3	136,666
142	36.8	26.2	171,818
Oyster Bay			
1	38.1	33.0	
2	40.6	30.5	
3	45.7	30.5	
4	38.1	30.5	
5	40.6	33.0	
6	45.7	35.5	
			Average 283,273
Mud Bay			
1	38.1	30.5	
2	38.1	30.5	
3	38.1	33.0	
4	38.1	25.4	
5	43.2	25.4	
6	35.5	27.9	
			Average 247,199

mens were counted separately. Two other counts were made, each of the combined larvae from six specimens, and the results averaged. In all, counts were made of 25 broods, which averaged 214, 642 larvae each.

The two sets of six broods each probably represent more accurately the fecundity of the standard market-sized oyster, for the specimens were selected as such and were larger than the average among the 13 specimens, the broods of which were counted separately. The number of larvae in a brood depends upon the size of the maternal oyster and upon the degree of "fatness," or amount of stored reserve nourishment, at the time the eggs are developing.

Most specimens which are carrying larvae have apparently spawned out almost completely, for the meats are generally watery and contain few eggs. This may be traceable to the alternation of sexual phases (Coe, '31a, '31b), while Galtsoff ('30b) noted that oviparous species discharge but a relatively small portion of the eggs at one spawning.

DEVELOPMENT OF LARVAE IN THE BROOD CHAMBER

It was pointed out above that the gestation period, or length of time that the larvae are held within the branchial cavity, has not been established for this species. The problem would be difficult to attack by direct observation in the laboratory, for gravid specimens are highly sensitive to disturbing factors and tend to abort the young larvae. When oysters are brought to the laboratory from the beds during the spawning season and placed in clean, running seawater they may be observed to discharge the young larvae. It would, therefore, not seem possible to determine the rate of larval development by taking daily samples from a single brood.

From an ecological point of view the problem is to determine the rate of development and the duration of the gestation period under natural conditions, on the oyster grounds. It was necessary to employ a statistical method to accomplish this. A small area of an oyster ground was selected and three or more times weekly 100 specimens were opened and the larvae from gravid individuals separately preserved in vials for laboratory examination. The larvae were studied microscopically and the size and stage of development recorded. In a single brood there is necessarily some difference in size of individual larvae, but this difference is surprisingly slight. In no brood were larvae of decidedly different stages of development found. There was no indication that an oyster might have spawned again while carrying a brood, although such might be possible if the first spawning should be incomplete.

It was soon noted that the number of oysters bearing larvae of the same age could be grouped together so as to form a definite unit, the development of the larvae appearing by frequent sampling of the population. For example, if on one day 10 oysters out of the 100 opened bore newly spawned eggs, on the following day approximately 10 per cent would bear embryos in the blastula stage. Naturally, complete statistical accuracy could not be approached by opening only 100 specimens at a time, but the studies were continued for a long time and the results are sufficiently clear to form the basis for definite conclusions.

This method has been employed on two to three different grounds, in different areas, during four consecutive seasons, and the results are typified by the series shown graphically in figure 1. In spite of the statistical error, the graph shows the rate of growth very satisfactorily. The average water temperature during the period varied from about 14° to about 19° C. (See fig. 3.)

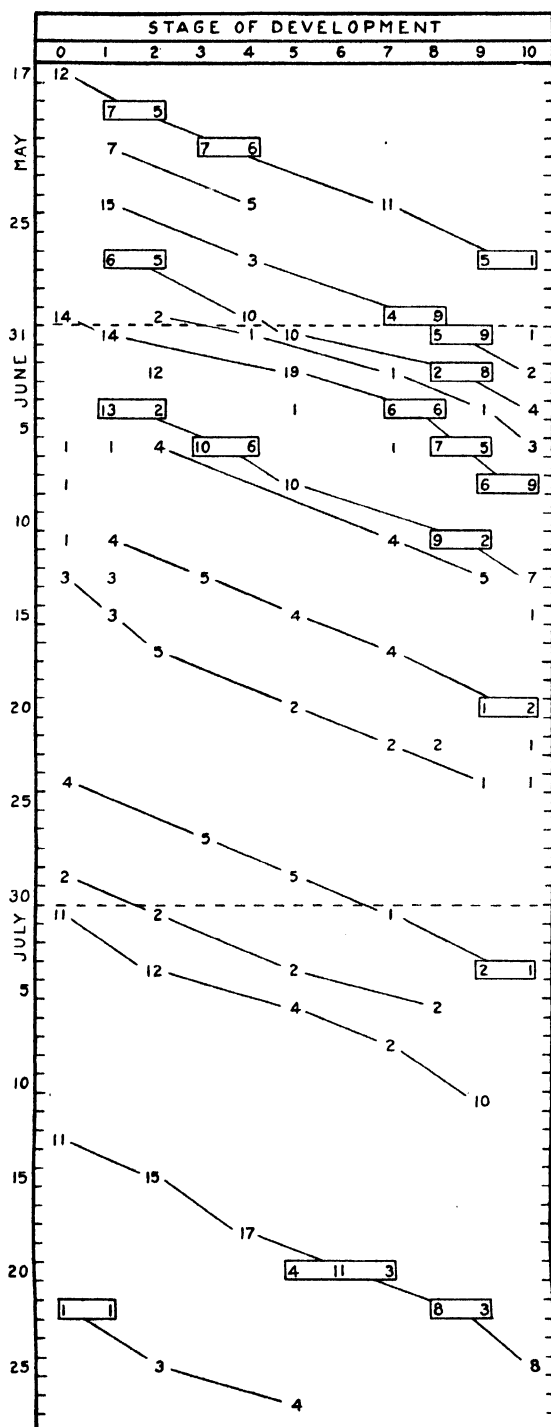


FIG. 1. Graph showing percentage of adults bearing larvae of various stages of development on different dates. The stages are defined as follows: 0, eggs or early segmentation; 1, blastulae; 2, gastrulae; 3, trochophores; 4, first conchiferous larvae, with incomplete valves; 5 to 10, straight-hinge veliger larvae of different lengths (in microns), approximately stated; 5, 110-120; 6, 120-130; 7, 130-140; 8, 140-155; 9, 155-170; 10, 170-185. The percentages of larvae of definite size groups are connected to indicate rate of development.

The diameter of the egg when spawned is 100 to 105 μ , as described by Stafford ('14) and Hori ('33), who published excellent figures of the developing larvae. At the time the larvae are discharged they have reached a length of about 175 to 185 μ . Increase in size does not begin until the earliest conchiferous stage is reached, about 4 days. During the first day, after discharge of the eggs from the gonad into the branchial chamber, a few segmentation stages may be seen. At the age of one day they are well developed blastulae, by the second day becoming gastrulae. The prototroch then develops by the following day as the larvae reach the active trochophore stage. On the fourth day the valves may be seen on the dorsal surfaces as clearly defined structures 30 to 40 μ in diameter. The valves then become complete and the resulting straight-hinged veliger larva slowly grows. The early embryos and larvae are pure white, but after the larval shell develops they become gray, then gradually darker until, at the end of the gestation period, they appear as a bluish black mass in the mantle chamber. Oystermen often refer to gravid oysters as "white sick" or "black sick" for this reason.

In general these observations appear not to be out of harmony with those of Stafford, save that instead of the 16½ days which he estimated, the present results indicate about 10 days. Coe's ('31a) estimate was, "a period of approximately 10 to 12 days, perhaps," under conditions obtaining near La Jolla, California. The gestation period may be considered as occupying from 9 to 11 days under the conditions obtaining on the grounds studied in the present work.

The length of the period during which larvae are carried by *O. edulis* has apparently not been completely determined, although Orton's ('26) work included an estimate based upon a system of sampling. He stated in his summary (p. 219), "An analysis of the spawning oysters into those with young embryos and those with mainly shelled larvae brings out the fact statistically that oyster larvae under natural conditions are retained in the mantle cavity a period of only 1 to 1½ weeks from the date of their extrusion as fertilised eggs from the parent. This observation is in concordance with extended field observations and experimental evidence of the attainment of the black-sick stage by an oyster in 5 to 7 days from the date of spawning."

Stafford used the word, *swarming*, to designate the final release of larvae from the maternal brood chamber, in contrast to the original spawning whereby the eggs are released from the gonad. Swarming in this species may, perhaps, be looked upon as the delayed completion of the process of spawning, which in oviparous species is completed at once. Whether swarming is accomplished by means of rhythmical contractions of the adductor muscle, as described by Nelson ('22) and Galtsoff ('30a) for spawning of *O. virginica*, is as yet undetermined. Stafford said the larvae gradually escape between the open valves of the adult.

THE SPAWNING SEASON

As the water over oyster grounds becomes warmer in spring the reproductive cells develop as a thick mass surrounding the visceral organs. There appears to be a certain minimum, or critical temperature below which spawning will not occur. Through the extensive investigations of Stafford ('13), Churchill ('21), Gutsell ('24), Nelson ('28*a, b, c*), Prytherch ('29), Galtsoff ('30*a*, '32), and others, it has been established that the minimal temperature for spawning of the female of *Ostrea virginica* is 20° C., and that little or no spawning occurs below this level. According to Galtsoff the critical temperature for the discharge of eggs by *O. gigas* is 25° C., though Elsey ('33) stated that spawning could be initiated by addition of sperms at 22° C. However, there is much still to be learned about the latter species in this respect, for the writer has observed spawning by females at temperatures as low as 8° C., though such may not be normal. Orton ('20) stated that the European oyster, *O. edulis*, spawns when the water temperature reaches 15° to 16° C.

In *O. lurida*, Coe ('31*a*) found spawning whenever the water temperature was as high as 16° C. Hori ('33) stated that spawning begins when an average temperature of about 14° C. is reached, and ceases at about 20° C. The average water temperature at which spawning begins in spring may depend upon the degree of maturity of the sexual products, for it was noted (Hopkins, '31) near Galveston, Texas, that the temperature of the water rose very rapidly and averaged about 25° C. before spawning of *O. virginica* started. Such a factor may be responsible for the discrepancy between the estimates of Coe and Hori, for the results of the present investigation are in closer agreement with the latter.

Records of water temperature in one of the most important oyster-producing bays were obtained by means of a thermograph. The instrument was fixed on a stand above the high tide level but the sensitive bulb was on the bottom at the level of the oysters. The oyster beds in this region are surrounded by dikes which maintain up to about six inches of water over the oysters to protect them from freezing and drying. The bulb, therefore, was always under water, and the thermograph record is an accurate measure of all temperature conditions to which the oysters are subjected.

Orton ('26) concluded that spawning of *O. edulis* takes place primarily during the full-moon tidal period, though he was uncertain as to the specific factor concerned. In a thorough investigation of *O. virginica* in one locality Prytherch ('29) concluded that, "the majority of the oysters spawned at the end of the July 'full-moon tidal period,' when the water was brought to a favorable spawning temperature." He expressed the opinion that at low tide when the water is warmest the oysters do not spawn because of the lower pH (7.2) as compared with a pH of 8.2 at high tide. Spawning, therefore, begins when the high tide temperature reaches 20° C. Nelson ('28*a, b*) concluded that there is a definite relationship between the rapidity of rise in tem-

perature after the high-tide temperature reaches 20° C. and the time required for the initiation of spawning. He found that in *O. virginica* during several seasons spawning started from 52 to 94 hours after the temperature of 20° was reached, depending upon how rapid was the subsequent rise. That a marked rise in temperature will induce spawning was shown by Galtsoff ('30b, '32).

In the case of *O. lurida*, the diked grounds in which the oysters are grown are all above the low tide level and the variation in pH and salinity with the tides is not great. As the tide goes out the heavier, more saline water tends to remain in the dikes while the surface water of lower salinity and pH runs off. In general, during the spawning season, the pH range is from 7.9 at low tide to 8.2 at high tide, and the maximum range observed during a 24-hour period is 7.8 to 8.4. It may be that, for this reason, the oysters may spawn at low tide also, for it has frequently been observed that specimens bearing newly spawned eggs were to be found after the dikes had been exposed to the warm sunshine for several hours.

Variations in water temperature in the dikes depend upon the range of tide on any particular day and upon the weather. In figure 2 are records of tem-

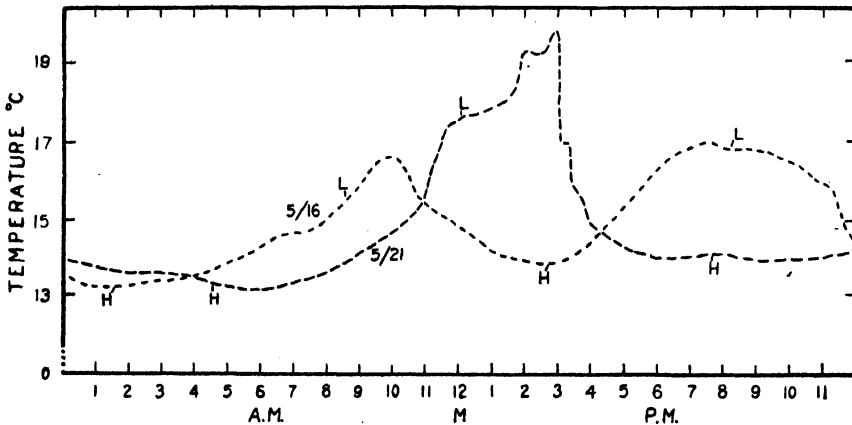


FIG. 2. Temperature records, transcribed from thermograph charts, showing variation in water temperature on oyster beds over two 24-hour periods: the former of the day (5/16) preceding discovery of the first gravid specimens (neap tide), the latter referring to the temperature five days later (5/21) when the dike was exposed for several hours at low tide. Times of low and high tides are indicated (L and H).

perature for two complete days. In both cases the minimum high-tide temperature was about 13° C., though at low tide when the water was shallow it became much warmer. The variation is due partly to the penetration of sunlight, partly to the fact that ebb tide brings water from the shallower, warmer areas up the bay. The effect of the two factors may be noted in the figure. On the day following the earlier record the ground was exposed at low tide

and the first gravid specimens, 12 out of 100, were found bearing early embryos.

In order better to illustrate the relationship between tidal cycles, water temperature and spawning activities, two graphs are reproduced (figs. 3 and 4).

The tidal cycles (figs. 3 and 4) refer not to the typical alternate high and low tides, which occur almost twice a day, but to the height of the two daily low tides. High tides are not included. When the heights of the two daily low tides are plotted graphically it is noted that the points fall into two separate series which come together, during neap tides, and become farther apart during extreme spring tides. On the figures, the trend lines are given to indicate the days on which the oyster grounds were exposed at the lower low tides. Most dikes are exposed when the low tide falls to the zero level. During a period of spring tides, when the lower low tides are below zero, the higher low tides may be at a level of 6 to 8 feet. The zero level is defined as the mean of the lower low tide heights. These records are included in the graphs to indicate possible correlation between tidal cycles and water temperature. It is to be noted that the extreme low tide periods, involving the absorption of heat from air and sunshine, frequently involve a rise in both average and minimum temperature. Because of this, the highest average and minimum may often be observed during neap tides, following a period of extreme low tides, when the total tidal difference is slight and there is relatively little mixing of the warm bay water with the colder water from deeper areas. As explained below, spawning is initiated by a maintained high temperature, rather than by a temporary condition.

In figure 3 (1932) it will be noted that at the beginning of April the average water temperature was about 9° C., from which it rose to about 12° by the end of the month. In the first half of May, during the period of low spring tides, the temperature rose to about 14° C., and on some days was higher. On the 17th, twelve out of 100 oysters bore embryos in the early segmentation stages in the mantle chamber. Within the next two weeks spawning activity developed to its maximum, when 55 per cent of the adults were gravid. During this time the average temperature had continued to rise slowly. The beginning of spawning is closely correlated with the sudden rise in the minimum, or high-tide, temperature which occurred on the 16th. On the 15th the minimum was 12.3° and on the next day, 13.2° C. At the same time the average rose to nearly 15°, but some days before this the average had been almost as high without initiating spawning, though the minimum was much lower. Through the remainder of the summer the average temperature gradually rose to about 20°, the minimum to 17°-18° C.

In 1933 (fig. 4) the picture was somewhat different in certain respects. Although the temperature on the first of May was slightly higher than in the preceding year, it rose only very gradually. The minimum remained almost constant at about 12° until nearly the end of the month when it gradually rose to about 13°. There was no sudden rise at this critical level

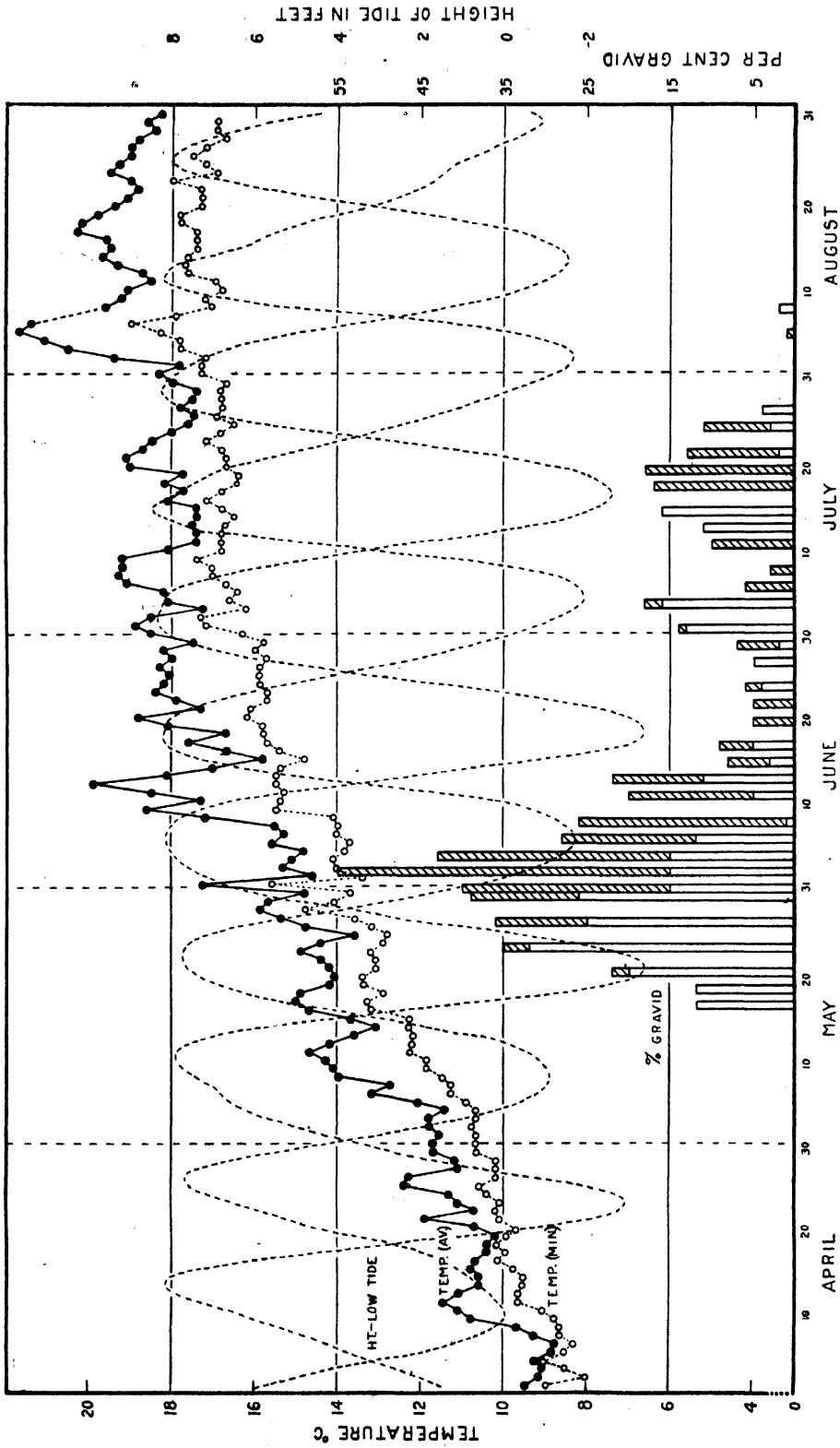


FIG. 3. Graph showing the percentage of adult oysters bearing larvae during the season of 1932. Shaded portions of columns indicate conchiferous larvae, open portions the earlier stages. Average (solid points) and minimum (open circles) temperatures are given over the same period, and the cycles of low tide heights are indicated.

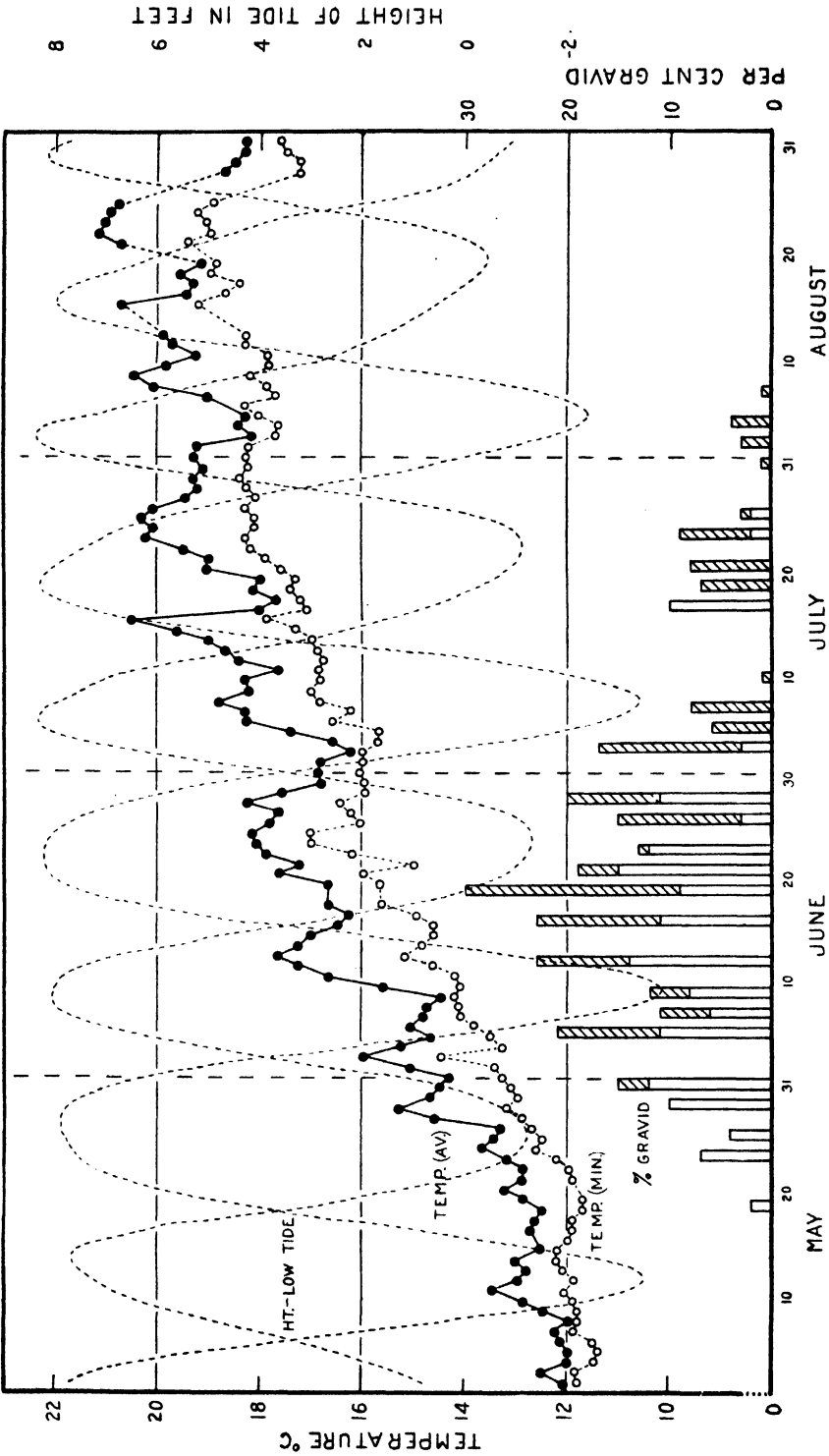


FIG. 4. Graph showing the percentage of adult oysters bearing larvae during the season of 1933. Shaded portions of columns indicate conchiferous larvae, open portions the earlier stages. Average (solid points) and minimum (open circles) temperatures are given over the same period, and the cycles of low tide heights are indicated.

as in the previous year, and although a few gravid specimens were found beginning on the 19th they disappeared from the collections, presumably by abortion due to low temperature at high tide. The actual beginning of effective spawning, judging by their continued growth, must be placed at about the 25th. This corresponds to a minimum temperature of about 13° and an average of between 13.5° and 15° . Considered in this manner, the two instances described in figures 3 and 4 are essentially identical.

The conclusion of Nelson ('28a, b) and Prytherch ('29), that spawning of *O. virginica* is initiated by the adequacy of the high-tide temperature, would appear to apply to this species also; although later in the season, when the minimum temperature is well above the critical level, spawning may occur at any tide. This is, perhaps, to be expected, since Prytherch noted that the spawning took place in a sudden burst of activity, which contrasts markedly with the gradual wave of spawning shown in figures 3 and 4. The present results suggest that the critical temperature for spawning by the active females of the species, *O. lurida*, is approximately 13° C.; by which it is meant that the lowest temperature during the tidal cycle is equal to or greater than this value. It is obvious that initiation of spawning may not be traced to the maximum temperature, for on many days in advance of spawning in the two years described the temperature rose at low tide to levels of 20° to 25° C. Also, the average temperature is a variable depending upon the length of time of exposure of the dikes at low tide and the consequent effect on the entire day's average of a few hours of maintained high temperature (fig. 2). Records like those described have been obtained during four years and the results in other cases are comparable to the two examples shown in figures 3 and 4.

The duration of the spawning season and the proportion of oysters spawning at the same time appear to vary greatly depending upon the locality as well as upon the species. Prytherch ('29) described the sudden spawning in *O. virginica* as occurring on a single day when conditions of temperature and pH become favorable. The same species in other localities, in which water temperature is generally higher, may continue spawning for many months (Hopkins, '31). Stafford ('14) stated that during a season in British Columbia waters (Puget Sound) eggs were found in some individuals (*O. lurida*) from May 20 to August 20, and that the spawning period reached its maximum at about the middle of June. Coe ('31a) found that spawning of this species occurred during about 7 months of the year in southern California. Moebius ('83) referred to the long spawning season of *O. edulis* and said that as many as 20.6 per cent of the oysters may be gravid at once. He estimated that at least 44 per cent of adults produced broods. Stafford's results indicate a similar proportion of oysters spawning at once.

It was desired to determine by systematic examination the progress of spawning by functional females throughout the season. The records for two of the four years during which this was done are shown in figures 3 and 4.

The other two years are not significantly different from these. The figures indicate that although some gravid specimens may be found for two or three months the major portion of spawning activity is confined to a period of about six weeks early in the season. Even in September and October an occasional oyster may be found bearing larvae. Most striking, in the two examples here presented, are (1) the clear difference between the proportion of individuals bearing larvae during different years, and (2) the difference in the general form of the curves.

In 1932 (fig. 3), spawning was very prolific, and at one time as many as 55 per cent of the adults bore larvae. By examining the results of this year (fig. 1), as recorded according to age of the larvae, it is possible to reach a conclusion as to the percentage of adults which produced larvae during the season. For this year the total is between a minimum of about 150 and a maximum of about 180 per cent. That is, all of the oysters produced one brood, and at least half of them bore a second brood.

On the other hand, in the following year (1933, fig. 4) the maximum proportion of gravid specimens at any one time was only about 30 per cent. The duration of the entire significant spawning period was about the same as that of the preceding year, but few individuals bore larvae at any part of the period. By totaling, from the original records, the number of spawners, the conclusion is reached that only about 75 per cent of the individuals bore larvae, possibly even less. Therefore, in 1932, at least twice as much spawning activity took place as in 1933. Similar analyses made on other grounds are in entire agreement with these results, so they are considered to be approximately accurate.

The frequency of spawning throughout the two seasons presents a decided contrast. In 1932 (fig. 3) spawning rapidly rose to a high peak within about two weeks, after which it dropped to a low level in about the same period of time. Later there was a small increase, reaching about 17 per cent gravid at once, though the later spawning was much lighter than the original. In the following year the results (fig. 4) might almost be represented as a single uniform curve, with only a small amount of late spawning; and the early spawning never reached a high level.

DISCUSSION

The small, monoecious, viviparous native oysters of the Pacific coast carry the developing larvae within the branchial chamber, adjacent to the palps and anterior ends of the gills, for a period ranging generally from 9 to 11 days under temperature conditions obtaining in the southern portion of Puget Sound. The number of larvae in a single brood depends upon the size of the maternal specimen and is usually between about 250,000 and 300,000 in the market-sized oyster. Galtsoff ('29) stated that this species probably gains no advantage by holding the young larvae, for in their free-swimming phase they

are subjected to natural enemies and unfavorable environmental conditions for as long a time as are the larvae of *O. virginica*. It would seem, however, that by carrying the larvae through the early segmentation and embryonic stages the species protects the young during the time when their lack of ability to swim would render them unable to avoid being smothered by silt and organic growth. At the time they are discharged they are actively swimming veliger larvae with well developed valves.

The development of the gonads and discharge of germ cells are controlled by conditions of temperature and probably other factors. The present results indicate that discharge of eggs begins soon after the minimum water temperature reaches approximately 13° C., although at this time the average temperature may be 14° to 15° C. During four years spawning has begun when the high-tide temperature did not drop below about 13° C., apparently confirming the conclusion of Nelson ('28a, b) and Prytherch ('29) for *O. virginica* that spawning takes place at high tide, although the water may be warmer at low tide. Prytherch suggested that a high pH was essential to initiation of the spawning process, and the present results are not in disagreement with the hypothesis. However, in *O. lurida* it was noted that during the summer, when the minimum temperature is well above 13° C., newly discharged eggs may frequently be found in the brood chambers when the tide is low and the water has been 20° to 30° C. for several hours. The pH range during a tidal cycle in this place is only about half that studied by Prytherch, which may throw some light on the results.

During the spawning season as many as 55 per cent of adults were found to bear larvae at one time. Most of the broods are produced during about six weeks following the beginning of spawning, although some gravid specimens may be found during several months. The proportion of adults which produced broods, however, is highly variable during different years. For example, in 1932, the results indicate that at least one and one-half broods were produced per oyster, on the average. That is, all spawned once and at least half produced second broods. On the other hand, in 1933, not more than 75 per cent of the adults spawned at all. From the observations at hand it appears probable that about 100 per cent of the oysters spawn once as females during the average season.

It is not possible, with the present information, to state the length of a latent period required for spawning after temperature conditions become adequate, as did Nelson ('28a, b) for *O. virginica*. He stated that this latent period becomes shorter in proportion to the rapidity of the rise in temperature above the critical level. It is known, however, that male oysters will spawn at a much lower temperature than females (Galtsoff, '30a). In the protandrous (Coe, '31a) *O. lurida* it may well be that spawning of functional males begins some time before any female spawning and that the free sperms supply the necessary stimulus as soon as temperature and other conditions become adequate.

SUMMARY

1. The average brood of the Olympia oyster, *O. lurida*, of market size, is approximately between 250,000 and 300,000 larvae. Smaller specimens bear fewer larvae; extra large ones, more.

2. Under temperature conditions obtaining in the southern portion of Puget Sound, the larvae generally develop within the maternal mantle chamber (brood sac) for a period of 9 to 11 days;

3. The number of days required to reach the most significant stages of development following fertilization is as follows: 1, blastulae; 2, gastrulae; 3, trochophores; 4, early conchiferous stage, with valves just appearing and still incomplete; 5, valves completed and the larvae in the straight-hinge stage; 10, larvae about 180 μ long, ready to be discharged.

4. The first oysters bearing broods of larvae are found soon after the minimum (high-tide) water temperature reaches approximately 13° C., although the average temperature at the same time may be from 14° to over 16° C. The maximum, or low-tide, temperature is obviously not the immediate controlling factor.

5. The spawning period in southern Puget Sound may last for six months or more, but most broods are produced during a period of about six weeks at the beginning of the season.

6. The number of broods per adult oyster varies, from year to year, from 75 per cent or less to 150 per cent or more. In the latter case it is considered that second broods were carried by at least 50 per cent. It would appear that during the average season approximately all adults produce one brood.

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EFFECTS OF THE GREAT DROUGHT ON THE PRAIRIES OF IOWA, NEBRASKA, AND KANSAS *¹

J. E. WEAVER AND F. W. ALBERTSON

The University of Nebraska

The response of prairie vegetation of eastern Nebraska during the great drought of 1934 has been described (Weaver, Stoddart, and Noll, '35). The purpose of the present study was to determine the results of the drought during the following year. The work has been extended to include the mixed prairie of west central Kansas.

Studies in Tall-Grass Prairie

The most severe drought ever recorded in the prairies of eastern Nebraska, western Iowa, and Kansas occurred during 1934. Studies of water content of soil throughout many growing seasons show clearly that the drought came on gradually during a period of 3 or 4 years. Water content of the upland was slowly depleted and by July 30, 1934, no water to a depth of 4 feet was available for growth. During July of this abnormally hot growing season, the average weekly maximum daily temperature varied from 98° to 111° F. The average weekly minimum daily humidity varied from 15 to 22 per cent. During certain afternoons the humidity was only 3 to 5 per cent. Drought swept from hilltops down the slopes into mesic and hydric ravines. Wilting, drying, and death of vegetation were not due alone to high temperatures and low humidities but primarily to low water content of soil, since plants in watered areas thrived.

Complete records of environmental factors in the prairie are being published elsewhere (Noll, '35); water content of soil available for growth before, during, and at the close of the drought are shown in figure 1. Hygroscopic coefficients of the Carrington silt loam, which ranged between 10.8 and 13.4 per cent at the several depths, were used as the approximate point of non-availability. Samples from which the data were compiled were taken from a typical upland, little-bluestem prairie on a gentle south slope near Lincoln. The abundant water supply in early spring in the first 2 feet was greatly reduced during May and entirely depleted by midsummer. The moderate to

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small reserves of the deeper soil in spring were likewise greatly reduced in June and entirely depleted in August to a depth of 4 feet, the deeper soil to 6 feet retaining less than 2 per cent available moisture. Drought continued during the winter and was not ameliorated until the following April. By June, subsoil moisture had been replenished to a depth of 6 feet. Below 6 feet depth moisture was constantly available throughout the drought, but in small amounts only.

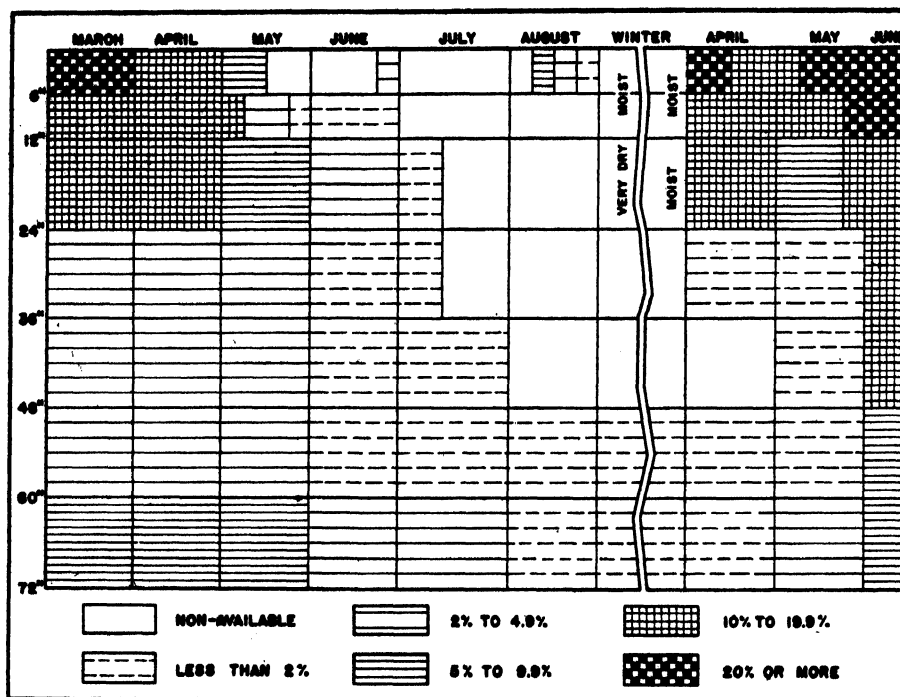


FIG. 1. Available water content of prairie soil near Lincoln, Nebraska, at the several depths to 6 feet, from March, 1934, to June, 1935.

A close relationship was found between root depth of most prairie grasses and resistance to drying. Among the forbs, resistance to drought was closely correlated with root extent. Species with root systems penetrating 8 to 20 feet into the moist subsoil were little affected. Many other species wilted and dried. This is in accord with the investigation of Nedrow ('36) who found a direct relationship between the amount of growth of tops of important prairie grasses and the depth at which water was available for absorption. When water was available only at a depth of 3 or 4 feet, some development of tops still occurred. Certain forbs grew normally when water was available only at depths below 3 to 5 feet.

PRAIRIES NEAR LINCOLN

Destruction wrought by drought in a group of prairies near Lincoln varied in degree but is well represented by the following descriptive and quantitative studies.²

Valparaiso prairie

A prairie one-half square mile in area covers hilly land 3 miles west of Valparaiso (fig. 2). In 1930, *Andropogon scoparius*, little bluestem, dom-

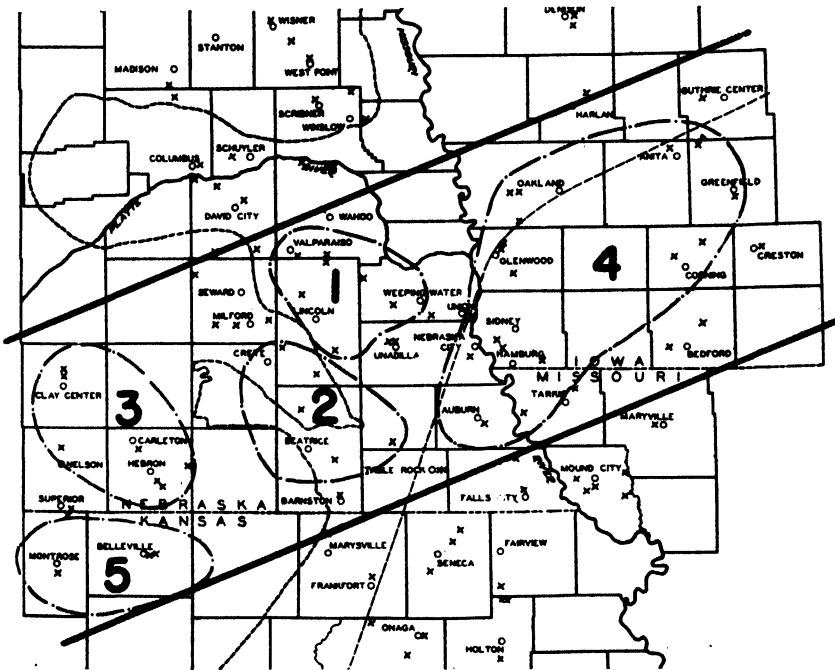


FIG. 2. Outline map showing groups of prairies (marked x) studied (1) about Lincoln, (2) south of Lincoln, (3) southwest of Lincoln, (4) in western Iowa and southeastern Nebraska, and (5) in north-central Kansas. The subdivisions are counties and the circles indicate towns or cities. The broken line across the southeastern part indicates approximately the isohyet of 32 inches. The tortuous line from north to south separates the Prairyerths on the east from the Blackerths on the west.

inated the hilltops, forming 60 to 90 per cent of the vegetation. *A. furcatus*, big bluestem, occurring in small tufts or as individual plants, frequently to the extent of 10 to 15 per square meter, was found in every one of a score of quadrats. *Poa pratensis*, bluegrass, was present to the extent of 1 to 3 per

² Prairies used for drought studies were the same as those employed in the investigations on "The Prairie" (Weaver and Fitzpatrick, '34). Since each of the prairies was earlier studied and described as a unit, the changes wrought by drought were readily determined. For purposes of comparison, a condensed statement of former conditions is sometimes included in this paper.

cent; *Sorghastrum nutans*, Indian grass, occurred in small amounts as did also *Bouteloua curtipendula* and *B. gracilis*. *Carex pennsylvanica* was well represented. Alternates of *Sporobolus heterolepis* with little and big bluestem, *Koeleria cristata*, and bluegrass were common on the drier ridges. A good understory of minor grasses and forbs was common throughout. The basal cover varied from 11 to 18 per cent. Halfway down the north-facing slopes and still lower on the south and southwest hillsides big bluestem increased to 30 to 40 per cent, blue grama and other xeric species disappeared. On lower slopes and in ravines, big bluestem constituted 80 to 90 per cent of the cover; *Panicum virgatum*, Indian grass, and bluegrass were the other important species.

This prairie had been visited annually. Few noticeable changes occurred until 1933, but marked ones during 1934. In the early summer of 1935, quadrats on the hilltops, where drought had been most severe, showed a loss of 45 per cent of the basal cover. A large series of random quadrats gave a reduction of 20 per cent over the upper north slope. Careful estimates of losses for the highest lands varied from 10 per cent where damage was least to 25 for the area as a whole. On lower midslopes average losses decreased to 12 per cent, and on still lower areas only traces of destruction by drought were found.

Little bluestem, bluegrass, and the interstitial *Panicum scribnerianum* and *P. wilcoxianum* had suffered most. *Sporobolus heterolepis*, dropseed, had also been much damaged, and dead bases and rhizomes of big bluestem, Indian grass, and most other species were also readily found. Seedlings of *Koeleria cristata*, June grass, were abundant, as were also those of *Kuhnia glutinosa* and *Erigeron ramosus*. Blue grama grass and *Carex pennsylvanica* were spreading and *Agropyron smithii* was also readily invading the areas bared by the death of the bluestems and other grasses. Wheat grass often grew in the dead bunches of these dominants. *Antennaria campestris*, young plants of *Helianthus rigidus* and *Solidago glaberrima*, and various other shallowly rooted plants had nearly all been killed by the drought.

Silene antirrhina was common everywhere as were also small amounts of *Lepidium virginicum*.³ *Aster multiflorus*, likewise profiting by the thinning of the prairie sod, had spread rapidly by underground parts. Bulbous species and others with fleshy underground parts or very deep root systems had usually sustained the smallest losses. On lower slopes and level ground, losses were similar in character but much smaller in amount.

Belmont prairie

The 160-acre Belmont prairie at Lincoln is representative of numerous others of eastern Nebraska. The little-bluestem type, alternating with *Stipa spartea*, needle grass, on the ridges and big bluestem in the ravines, has been

³ Probably *L. densiflorum* in part.

described (Weaver and Thiel, '17). Losses from drought varied greatly with slope and exposure as well as with degree of burning, frequency of mowing, etc. In general, any protection afforded by dead cover was distinctly favorable to both soil and vegetation. Plants on unburned portions of the prairie mowed but once annually, which is the usual practice, suffered least.

A large series of quadrats for determination of basal cover in 1930 to 1932 gave an average of 9.2 per cent but in 1935 the basal cover in the same area was reduced to 5.9 per cent, a loss of 36 per cent (figs. 3 and 4).



FIG. 3. Selected sods of *Andropogon scoparius* on June 19, 1935, showing various degrees of loss by drought from 0 (upper left where the grass is 16 inches tall) to 100 per cent (lower right). Note the retarded development where most of the bunch died.

The major losses were of the nature of "holes" or openings in the prairie cover, a condition greatly emphasized because of the unusual development of the foliage early in 1935 (figs. 5 and 6). Superficially the prairie appeared normal—to appreciate the losses one had to penetrate the foliage and study the basal cover. In the moderately affected areas, spaces bare of living plants were more or less isolated. Each, however, bore its toll of dead crowns of little bluestem or dropseed, rhizomes of big bluestem and Indian grass, usually exposed by erosion of wind or water, the paler stem-bases of needle grass and bluegrass, or remnants of other species.

Often these openings were marked by dense patches of annuals or short-lived perennials. Most important of these were *Lepidium virginicum*, *Tragopogon pratensis*, *Silene antirrhina*, *Specularia perfoliata*, *Festuca octoflora*, and *Erigeron ramosus* (figs. 7 and 8). But many such areas remained bare throughout the entire summer. These openings in the grass cover were conspicuous throughout the growing season. A dry spring retarded early growth, a moist early summer promoted unusual development of established plants which caused so dense a shade as to inhibit development of seedlings. In fact,



FIG. 4. Normal development of *Sporobolus heterolepis* (upper row) and *Andropogon furcatus* (lower row) on left, and progressive destruction by drought.

with a loss of one-third of the basal cover, the cover of foliage appeared nearly as great as during a normal year for growth. The weedy annuals, where they had invaded, all died in June but remained intact almost throughout the summer.

Where drought was more severe the open spaces were more plentiful and formed a very irregular network of unoccupied soil surface. This was beautifully illustrated in many alternates of *Stipa*. Often most of the smaller, less deeply rooted bunches succumbed as did the accompanying bluegrass, little



FIG. 5. An opening in the tall-grass cover resulting from drought, showing dead *Andropogon scoparius* and *Poa pratensis*, and bare soil. *Stipa spartea* and *Koeleria cristata* in background, *Poa* on the left, and *Tragopogon pratensis* and *Silene antirrhina* on the right. Photo at Belmont, June 7, 1935.



FIG. 6. Opening in the cover of *Andropogon scoparius* near Lincoln, resulting from drought. June 7, 1935.



FIG. 7. Invasion of *Tragopogon pratensis* into upland prairie as a result of the death of much native vegetation by drought. Photo June 8, 1935.



FIG. 8. Normal abundance of seedlings of *Erigeron ramosus* in areas left open by the death of *Andropogon scoparius*. Photo June 6, 1935.

bluestem, etc. The excellent development of the widely spaced, remaining clumps produced a fine foliage cover 2.5 to 3 feet high, often with 40 stems in a single bunch, although beneath large irregular open spaces were continuous. Thus openings of moderate size graded imperceptibly into larger areas a square meter or more in extent, also destitute of living plants. Finally, the cover was so decimated that the terrain appeared almost bare with only the remnants of a former population. Where invasion by prairie forbs, such as *Aster multiflorus*, *Solidago glaberrima*, and others, liberated from competition, was pronounced or where annuals were present in abundance, the prairie had the ragged appearance of a weedy pasture. Here the percentage of remaining prairie sod was small.

Losses on many uplands were only 10 to 25 per cent and a good matrix of the native grasses remained. In others over half of the bluestems, etc., had been swept away and forbs, except deeply rooted ones, had suffered similar losses. In a few cases, where the glacial soil was thin and gravelly, the bluestems, Indian grass, bluegrass, and other less xeric species were practically exterminated and only needle grass, blue grama grass, *Bouteloua gracilis*, and remnants of slender grama grass, *B. curtipendula*, with certain forbs, remained.

Great destruction to species of the understory gave the grassland its distinctly open appearance. Among these species, the following were most conspicuous: *Poa pratensis*, *Panicum scribnerianum* and various other species of panic grasses of low stature, *Eragrostis pectinacea*, and *Agrostis hyemalis*. *Antennaria campestris*, *Viola pedatifida*, *V. papilionacea*, and species of *Polygala* were forbs which suffered great losses. The same was true of *Gentiana puberula*, *Senecio plattensis*, species of *Physalis*, and rosettes of *Hieracium longipilum*.

Koeleria cristata was sometimes extremely abundant in burned prairies. The bunches frequently had 20 to 40 flower stalks and grew in the little-bluestem sod as thickly as 35 to 40 per square meter. *Agropyron smithii*, wheat grass, which formerly occurred very sparingly, made notable increases. These were most conspicuous along roadsides and in pastures where it became extremely common but it also invaded prairies. At first the stand was thin and the stalks scattered, but soon it consolidated its holdings into dense stands of 1,500 or more stems per square meter. Such potential centers of wheat grass are now common on the uplands and even more abundant on lower ground. Amount of future precipitation will determine its advance or decrease.

Results from quadrats

Numerous permanent quadrats were established, mostly on the Belmont Prairie near Lincoln, but also at Weeping Water, about thirty miles eastward, and elsewhere. These were charted during September of 1934. For clarity each quadrat usually denotes only the dominant species or two or three domi-

nants. All of the major grasses (Weaver and Fitzpatrick, '34) were included in enough quadrats so that their recovery or lack of recovery was determined.

Selected quadrats illustrating the chief conditions and changes are shown in figures 9 to 16. Scores of quadrats were used, however, in making deter-

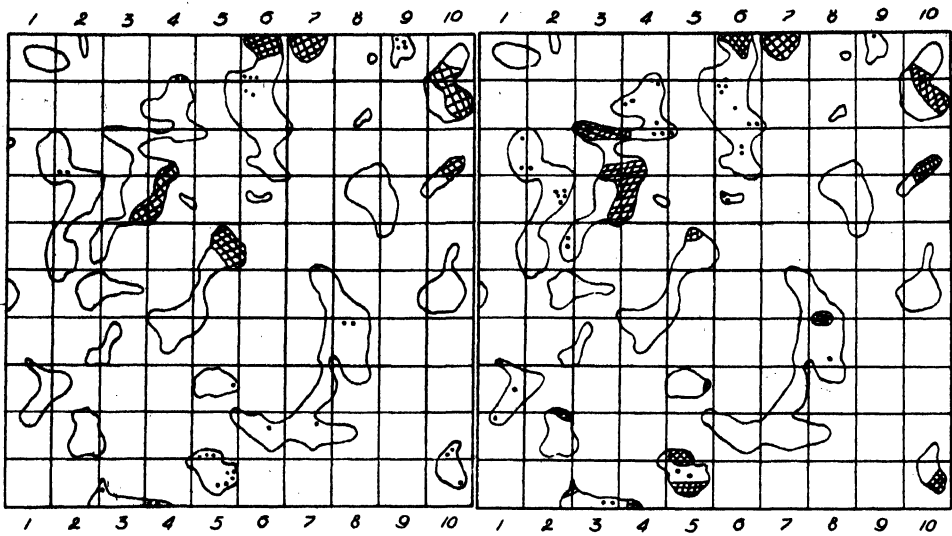


FIG. 9. Quadrat on hilltop in Belmont prairie in *Andropogon scoparius* consociation showing dead little bluestem (unhatched areas), living mats (cross hatched), and isolated stems (dots) in September, 1934 (left) and late in May, 1935 (right). Only 10 per cent of the grass was alive in fall but this increased to 17 per cent by the following June.

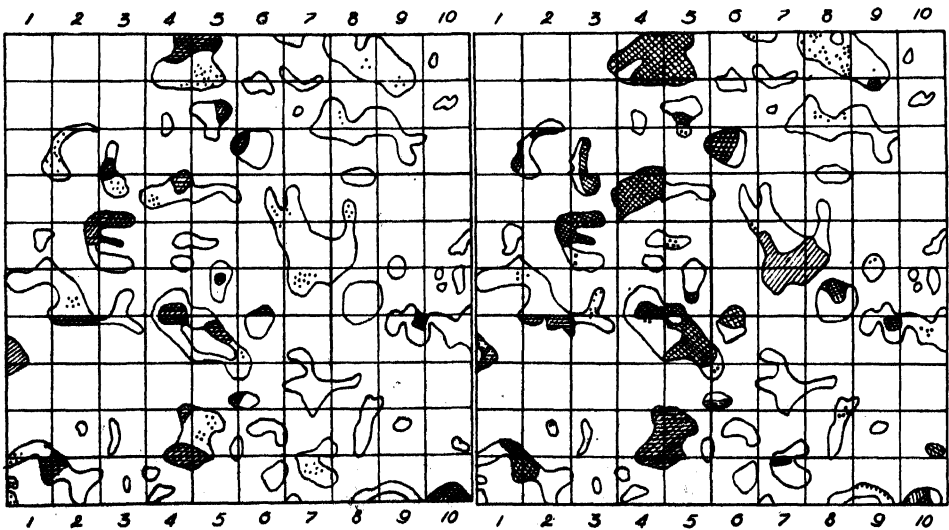


FIG. 10. Quadrat on upper north exposure in *Andropogon scoparius* consociation. Dead (unhatched), fully sodded (cross hatch), half populated (single hatch), and isolated stems (dots). Living plants occupied 15 per cent of the area of the bunches in fall (left) but 18 per cent in June (right). Thus recovery was somewhat less than on the hilltop.

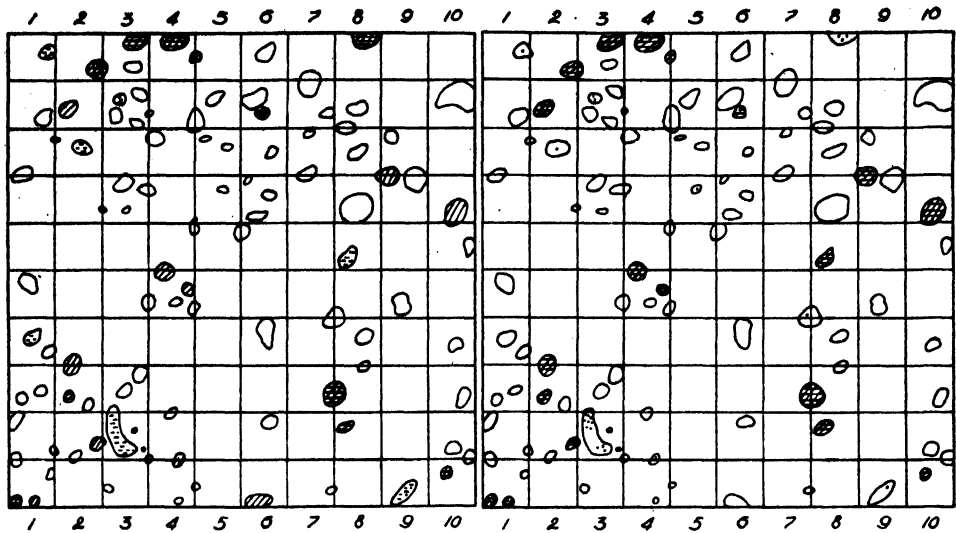


FIG. 11. Quadrat in needle-grass type on hilltop at Belmont showing dead (un-hatched), unharmed (cross hatched), half dead (single hatch), and nearly dead (broken hatch) bunches of *Stipa spartea*. Dots indicate isolated stems. Note the great loss of the smaller (younger) bunches and the slight recovery in spring (right).

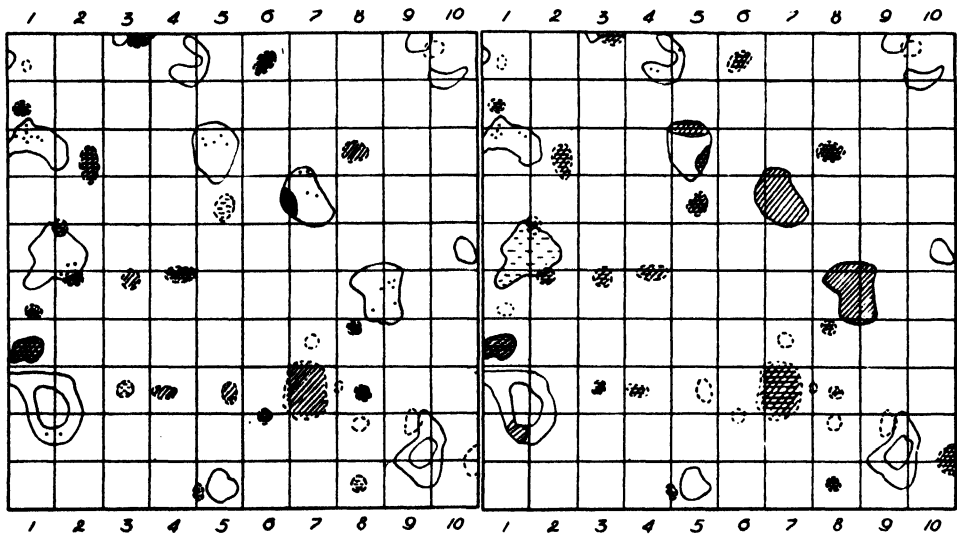


FIG. 12. Mixed bunches of *Stipa* (broken lines) and *Andropogon scoparius* (solid lines) in the fall (left) and following spring. Legend as in preceding figure. Needle grass withstood the drought much better than did little bluestem.

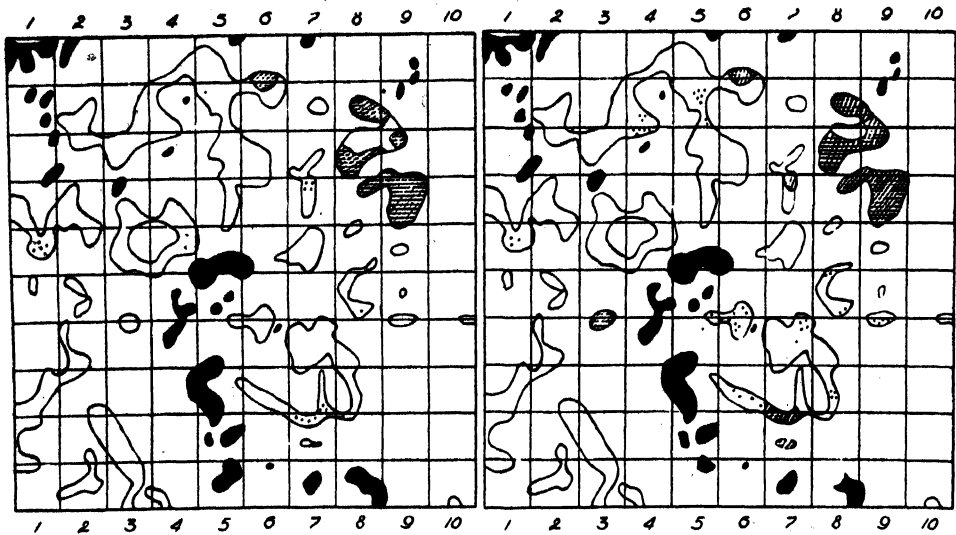


FIG. 13. *Sporobolus heterolepis* and living *Bouteloua gracilis* (black) in Belmont uplands in September (left) and in the following June (right). Prairie dropseed had suffered a loss of 85 per cent. Small winter losses of blue grama occurred.

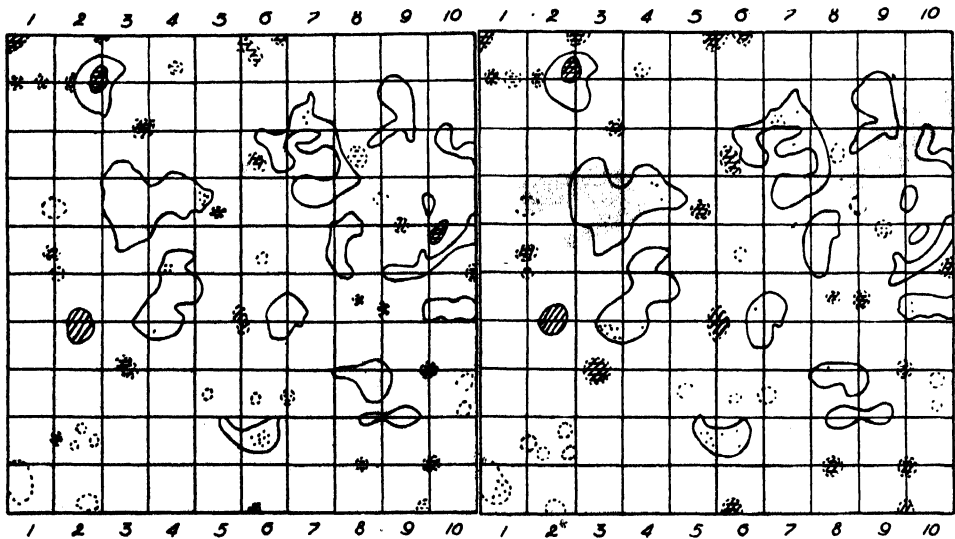


FIG. 14. Quadrat of *Stipa spartea* (broken lines) and *Sporobolus heterolepis* (solid lines) on south slope. Note that many bunches of both species are dead (unhatched) or contain only a few isolated stems (dots). Half-dead bunches are indicated by single hatch and unharmed ones by cross hatch. Losses were 35 and 93 per cent for the two species, respectively, and recovery of both was slight.

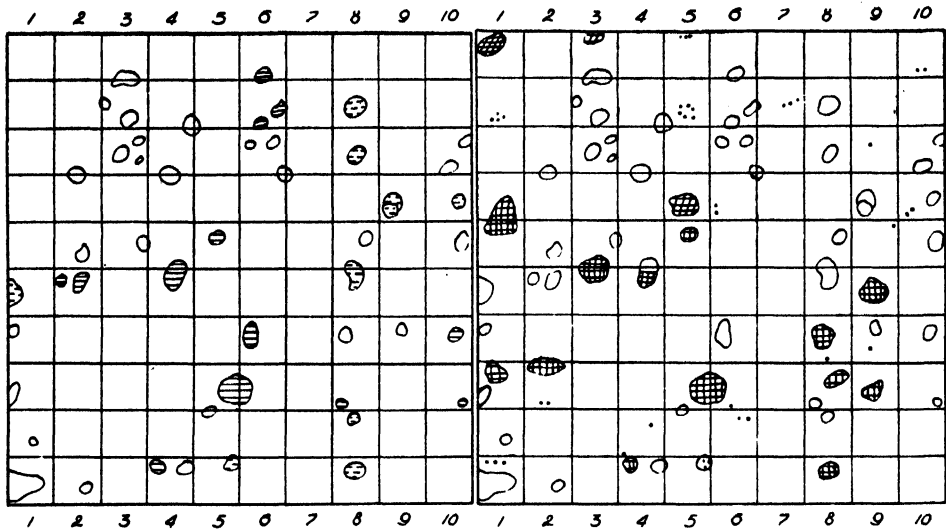


FIG. 15. Quadrat on level upland nine miles west of Lincoln, showing death of *Andropogon furcatus* in fall of 1934 (left) and new growth from rhizomes in May, 1935. Dead indicated by unhatched, nearly dead by broken hatch, half dead by horizontal hatch, unharmed by cross hatch and isolated stems by dots. Many new tufts were formed during the moist spring.

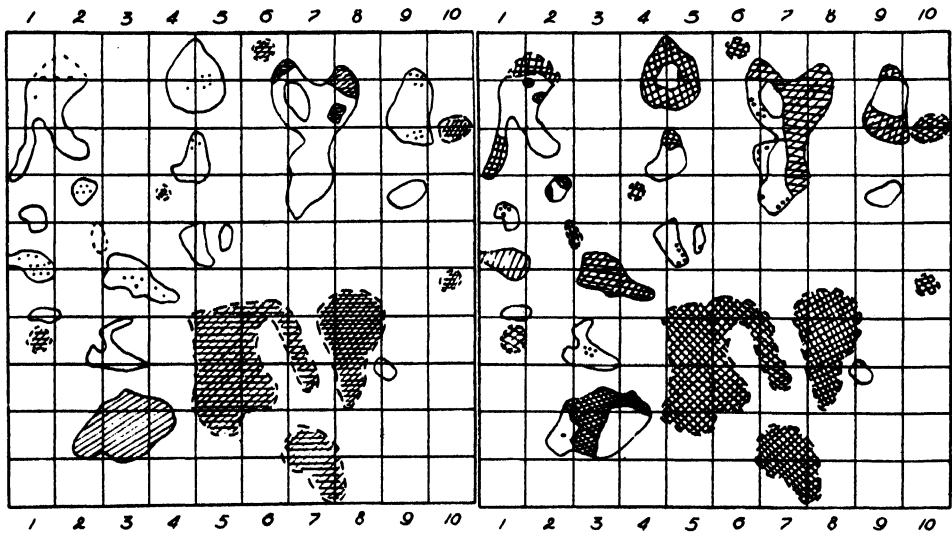


FIG. 16. Bunches of *Andropogon scoparius* (solid lines), *Sporobolus heterolepis* (long broken lines), and *Stipa spartea* (short broken lines) in Belmont prairie. In the fall (left), 82 per cent of *Andropogon* appeared dead but the following June only 48 per cent was dead (right). *Sporobolus* and *Stipa* suffered only slight injury and no loss.

minations of losses. The moist, late spring and early summer of 1935 promoted an excellent growth of plants that were not dead, hence there was a clear line of demarcation between the living and dead portions of the bunches and sod mats despite the fact that those nearly killed by drought grew slowly.

Little bluestem suffered the greatest losses of all the grasses, not only at Belmont but also throughout the entire area. It succumbed on many xeric ridges where *Stipa spartea* and *Bouteloua gracilis* largely survived. The losses of *Poa pratensis* were heavy except where it was well protected by dominant grasses. Thus in burned areas and bluegrass pastures it was nearly all dried by May 15, 1934, and little revived the next season. But under the shade of other vegetation it remained green much longer and often survived the drought. Its habit of midsummer semidormancy was distinctly beneficial.

Stipa spartea lost most of its younger, less well established bunches, but otherwise resisted the drought remarkably well. It flourished during the moist early summer of 1935 and produced an enormous seed crop.

Koeleria cristata, although greatly harmed by the drought, reproduced readily by seed. During 1935, although nearly absent in the drier western prairies, it was extremely abundant, of unusual stature, and seeded prolifically in many of those eastward.

Losses of *Sporobolus heterolepis* were somewhat less than those of little bluestem where these species were intermixed, this grass showing distinctly more xeric tendencies.

Andropogon furcatus, although in general much less xeric than *A. scoparius*, survived, in part because of its deeper root system extending into moist subsoil, in areas where little bluestem succumbed. Its losses, however, were great almost everywhere on uplands. It showed strong powers of recovery.

Sorghastrum nutans had taken fully an 80 per cent loss at Belmont and often more elsewhere. *Panicum virgatum* and *Elymus canadensis* also suffered great decreases. *Bouteloua curtipendula* showed marked xeric tendencies and, although suffering greatly, held on well and usually gave good recovery.

Spartina michauxiana showed great injury during the late summer of 1934 and was unable to hold its areas even during the two preceding years. As the soil dried with a lowering of the water table in ravines and lowlands, it slowly gave way to less hydric grasses and accompanying forbs.

Jamaica prairie

This prairie consists of 65 acres of rather low, level land lying north of a stream bordered by postclimax woodland 12 miles south of Lincoln. A portion of it covers the lower slope of a south-facing hillside. It was an excellent big-bluestem prairie, this species alone furnishing 60 to 90 per cent of the cover. Little bluestem sometimes constituted as much as 25 per cent

of the cover on the upland. *Sporobolus heterolepis* occurred in local alternes on lighter soil. *Sorghastrum nutans*, in addition to a 1 to 5 per cent mixture throughout, increased to 20 per cent or more where high waters sometimes overflowed. Slender grama grass was important on the hillside. *Poa pratensis* occurred as a 1 to 5 per cent sprinkling everywhere, but in many places increased to 15 per cent. In a few local alkali depressions occurred *Agropyron smithii*, *Bulbilis dactyloides*, buffalo grass, and *Bouteloua gracilis*.

Layering was well developed and over 70 species of forbs were listed. *Aster multiflorus*, *Solidago glaberrima*, *Rosa arkansana*, and *Gaura parviflora* were among the most important. *Artemisia gnaphalodes* and *Hedeoma hispida* were of less abundance, and *Specularia perfoliata* and *Silene antirrhina* were either infrequent or rare.

Examination during August, 1935, showed that a large alterne of wheat grass had developed. It was about 5 rods wide and extended across the prairie at the base of the slope after which it spread widely over the level ground. The wheat grass was 2.5 to 4 feet tall, the heads 6 to 8 inches long, and the stand dense (fig. 17). While the former grasses were all dead, some



FIG. 17. Lowland near Lincoln, Nebr., formerly dominated by *Andropogon furcatus* which has been entirely replaced, as a result of drought, by a thick stand of *Agropyron smithii*.

of the forbs especially *Rosa arkansana*, *Artemisia gnaphalodes*, and *Allium mutabile* still persisted. *Rosa* and *Solidago glaberrima* sometimes formed an open understory and *Silphium integrifolium* an overstory in this dry wheat-grass alterne. *Hedeoma hispida* nearly always accompanied the wheat grass.

Above the belt of wheat grass the bluestems and other grasses had been completely or almost completely replaced not only by dense growths of prairie forbs, especially *Artemisia gnaphalodes* and *Aster multiflorus*, but also by mixtures of many others. *Silene antirrhina*, *Specularia perfoliata*, *Gaura parviflora*, and *Hedeoma hispida* formed tangled growths. Accompanying or intermingled with these were dense patches of *Tragopogon pratensis*, *Lactuca scariola*, and *Lepidium virginicum*.

The prairie below the wheat-grass area, sheltered by the fringing woodland from the southwest winds, was in nearly normal condition. Most of the bluegrass and understory plants, however, had perished. Transition areas occurred, sometimes quite detached from the main ones but always on low ground where the wheat grass formed only half a stand and the bluestems were still abundant.

The remaining three-fourths of the prairie had suffered a great catastrophe. Wheat grass had claimed one-third, and the rest, except for a few relict patches, had been overwhelmed by weedy native or introduced forbs. Rarely only did the native grasses occur in this waste in excess of 1 to 25 per cent of the cover, and over most of the area there were none; many of the more mesic forbs were entirely absent although the more deeply rooted ones and those with bulbs, corms, etc., usually remained.

PRAIRIES SOUTH OF LINCOLN

A group of four large prairies south of Lincoln and representative of that portion of the area, were found to be greatly damaged by the drought.

Crete prairie

A brief description of 160 acres of prairie near Crete, Nebraska, will represent fairly well the destruction that had occurred in the whole group.

The Crete prairie consists of level upland and lowland, gently sloping hills, and ravines. On upland the chief dominants were little bluestem with only slightly smaller amounts of big bluestem and a considerable intermixture of prairie dropseed. The bluestems alone frequently constituted 80 to 90 per cent of the plant cover. In other places the dropseed formed 10 to 35 per cent. On lowlands big bluestem alone became the sole important dominant. Other grasses common but not abundant throughout were *Koeleria cristata*, *Stipa spartea*, and *Sorghastrum nutans*. Extensive quadrating also showed that *Poa pratensis* constituted 1 to 10 per cent of the basal cover and five species of interstitial panic grasses about 1 per cent. Only an isolated plant of *Agropyron smithii* was found here and there. Several ravines bore excellent stands of *Spartina michauxiana*. Forbs were common everywhere but none occurred in unusual abundance.

The dry year of 1933 initiated some changes in the plant cover and these were pronounced by August 1, 1935. After extensive study and measure-

ments it was ascertained that about one-half of the prairie—some lowlands, uplands with little run-off, and other favored places—had been affected by the loss of only 5 to 15 per cent of the vegetation. About one-fourth had lost 20 to 50 per cent, while over the remaining one-fourth the losses amounted to 80 to 98 per cent.

Little bluestem had taken the greatest losses among the dominants, prairie dropseed ranked second, and big bluestem had been much injured almost everywhere. Bluegrass had disappeared from one-third of the prairie, otherwise it was common. Interstitial panic grasses, formerly abundant, were not found. Indian grass and slender grama grass were represented by mere remnants. June grass, however, was about twice as abundant as normally, and needle grass had increased considerably.

Great gains had been made by wheat grass. Small alternes were common throughout the prairie, some were several square rods in extent; only the best remaining bluestem was not invaded. Aided by accumulated dust-blown soil in ravines, the former slough-grass area was now completely occupied by stands of wheat grass, so dense that no other grasses or forbs remained. Small patches of wheat grass often completely covered local areas of a few square yards with abundant flower stalks and then shaded out into surrounding areas of half dead bluestems. Here the growth was entirely vegetative, the invasion recent, and on the distant periphery of the area the stems were few. Only the tall, deepest rooted forbs remained alive in areas where wheat grass prevailed.

Aster multiflorus had spread widely until it constituted a dense, tangled, weedy growth over many acres. The plants were only 18 to 24 inches tall but very thickly distributed from the ever increasing rhizomes. Everywhere beneath them were the dead bluestems or living relicts of these and other prairie grasses. When the aster was removed the soil was almost bare.

The bare ground, and not the usual debris of accumulated stems, leaves, and bases of last year's grasses, was the prominent feature over at least half the prairie. In these bared places, resulting from extreme drought, the cracking of the soil was pronounced and rather general. The cracks were often one-fourth to three-fourths inch wide and several feet in length. Sometimes they were branched and crisscrossed in such a manner as to form large soil columns. Similar cracking of the soil was usual in the bared areas of most prairies, especially westward.

With the loss of the protecting cover of grasses, the understory vegetation practically disappeared. Such species as *Viola pedatifida*, *Fragaria virginiana*, *Physalis* spp., and others, although formerly common, were not found. The tall forbs, except young plants, were less affected.

Silene antirrhina, *Specularia perfoliata*, *Erigeron ramosus*, *Leptilon canadense*, *Lepidium virginicum*, and certain other weedy species were abundant.

Other prairies

In a prairie north of Beatrice, *Solidago glaberrima* had become a weed quite as widely spread as was *Aster multiflorus* in the Crete prairie. Blossoming at a height of 30 inches, it appeared as a continuous compact society with isolated, smaller ones over nearly 20 acres. On the ground were found the dead remains of the bluestem grasses.

Wheat grass was far more advanced in a prairie west of Beatrice. It had nearly complete possession of about 20 acres and outposts were well entrenched in every square rod of the remaining half. Death toll of the former



FIG. 18. Typical dense stand of *Erigeron ramosus* in drought-ravaged prairies of Nebraska. Photo July 6, Tecumseh, Nebr.

grasses had been heavy indeed, and many of the common forbs had been killed. Others, freed from competition, spread widely. These prairies, like those described, had not been pastured but mowed in autumn during the last 20 to 40 years.

In a prairie of 160 acres near Tecumseh, 33 miles northeast of Beatrice, the worst drought-stricken areas had been invaded most extensively by *Erigeron ramosus* and *E. annuus* (fig. 18). Great societies of these weedy forbs occupied nearly a third of the prairie. Wheat grass had invaded and was rapidly increasing as was also *Bromus secalinus*, but to a smaller extent. General destruction was similar to that described at Crete.

PRAIRIES SOUTHWEST OF LINCOLN

A representative group of prairies about 75 miles southwest of Lincoln and including large tracts near Clay Center, Nelson, Carleton, and Hebron were also studied.

Clay Center prairie

A slightly rolling upland prairie, 20 acres in extent, near Clay Center, was described as follows after continued study in midsummer of 1931. "A typical little-bluestem prairie with a tufted sod and sometimes bunchy growth of *Andropogon scoparius*. In many places this species affords 90 to 95 per cent of the cover. Elsewhere *A. furcatus* contributes 5 to 20 per cent, rarely more, of the stand. *Poa pratensis* and *Sorghastrum nutans* usually add 1 to 5 per cent to the basal cover but are often absent from the quadrats. There are only traces of *Stipa spartea* and *Sporobolus cryptandrus*. Small amounts of *Festuca octoflora* are found and *Agropyron smithii* is represented occasionally by single stalks. In limited areas in the ravines, big and little bluestem share the soil almost equally. On the drier slopes *Bulbilis dactyloides* and *Bouteloua gracilis* cover considerable tracts either as an understory to little bluestem or as alternates. Here *Koeleria cristata* is fairly abundant.

"The number of species of forbs is not large, nor, except for *Amorpha canescens*, are they very important. Of first rank are *Aster multiflorus*, *Eriogon ramosus*, *Artemisia gnaphalodes*, *Psoralea argophylla*, and *Solidago rigida*."

This prairie was visited again on June 27, 1935. Good crops of hay had been harvested during 1932 and 1933 but the prairie was greatly damaged by the drought of 1934. In the spring of 1935 great quantities of dust from the nearly level adjacent fields had blown in, especially from the south and west, and covered much of the area. In the ravine the new layer of soil was several inches deep; over much of the prairie it was two or more inches thick.

Not a single living plant of little bluestem could be found although the dead rhizomes were abundant under the new layer of soil. Big bluestem had persisted, however, on a part of the upland and especially in a long-abandoned prairie trail. The short grasses, where not thickly covered with soil, were thriving. *Koeleria* was blooming in isolated bunches.

Agropyron smithii formed a thin open stand over the areas covered to a moderate depth with dust and occurred in great alternates throughout in the shallower soil. It was densely aggregated in places. *Festuca octoflora* was very abundant in the bared area only shallowly covered with dust.

Deeply rooted forbs had sustained small injury; many were thriving in the absence of the competing bluestems. *Artemisia gnaphalodes* formed large societies as did also *Solidago glaberrima*. *Aster multiflorus* was rapidly increasing; *Meriolix serrulata* was abundant; and *Amorpha canescens* was thriving. Half buried *Liatris punctata* and *Solidago mollis* were observed.

Senecio plattensis, *Sisyrinchium angustifolium*, and other plants of small size or shallow root habit were not found. *Hedeoma hispida* was widely spread and abundant.

Much of the area had the appearance of an abandoned field, the remainder that of a weedy pasture. The following ruderals were abundant in the deeper new soil areas and common almost throughout: *Salsola pestifer*, *Amaranthus retroflexus*, *Chenopodium album*, *Lepidium virginicum*, *Leptilon canadense*, *Bromus tectorum*, *Setaria* spp., and *Echinochloa crus-galli*.

Thus in a 12-month period a thriving climax prairie had by drought and wind erosion been all but destroyed.

Carleton prairie

This is a nearly level upland prairie of 80 acres with a broad ravine running its entire length. The present owner homesteaded the land fifty-nine years ago. It has not been grazed but is mowed annually for hay. As was usual in the early days of settlement, a fire guard was plowed across the south end. This consisted of a strip of cultivated land about two rods wide which was annually planted to sorghum, maize, or some other tilled crop. The area was originally studied in 1931 and 1932.

Andropogon scoparius exhibited the sod-mat rather than the drier bunch type. It was the chief dominant, often forming 85 per cent of the cover, and always exceeding 60 per cent except on the lower land where its dominance was shared about equally with *A. furcatus*. Big bluestem constituted 20 per cent of the cover as a whole, increasing to 50 per cent or more on low ground, but sometimes decreased to 5 per cent on higher lands. Everywhere it exhibited the open-sod type, intermingling freely with the other grasses. *Agropyron smithii* was common in the ravine where it formed 25 to 33 per cent of the vegetation. Several small areas, each a few feet square, in the driest places were clothed with *Bouteloua gracilis* or, less frequently, with *Bulbilis dactyloides*. *Koeleria cristata* was generally distributed but only in 3 to 5 per cent abundance. Many areas were free or nearly free from *Poa pratensis* but in places it occurred in 5 to 15 per cent abundance. *Festuca octoflora* was not abundant anywhere.

The most important forbs were *Erigeron ramosus*, *Amorpha canescens*, *Artemisia gnaphalodes*, *Callirrhoe alceoides*, and *Aster multiflorus*. *Rosa arkansana*, *Solidago glaberrima*, and *Kuhnia glutinosa* were of less importance. *Hedeoma hispida* was found only accompanying the wheat grasses or short grasses.

During the dry years of 1933 to 1935, great changes occurred. The little bluestems suffered a loss of 95 per cent (fig. 19). In fact, it had met death almost everywhere except in the lowest places where it was protected by big bluestem. Losses of big bluestem were 10 to 15 per cent. Bluegrass remained only in the most moist places, but here it often occurred thickly.

No Indian grass was found. Certain other grasses, however, had made great gains, especially western wheat grass. Half of the entire prairie was now dominated by this species and one-fourth or more of the remainder was shared to the extent of 50 per cent. Less than one-fourth of the prairie was still held by the bluestems.

Wheat-grass alternes.—Over extensive areas wheat grass was three feet tall. In much of the territory where it was best developed all of the more mesic grasses (bluestems, bluegrass, and others) had been entirely swept away although their dead remains were still eloquent of former possession. Often the basal cover of wheat grass did not exceed 1 to 3 per cent. The

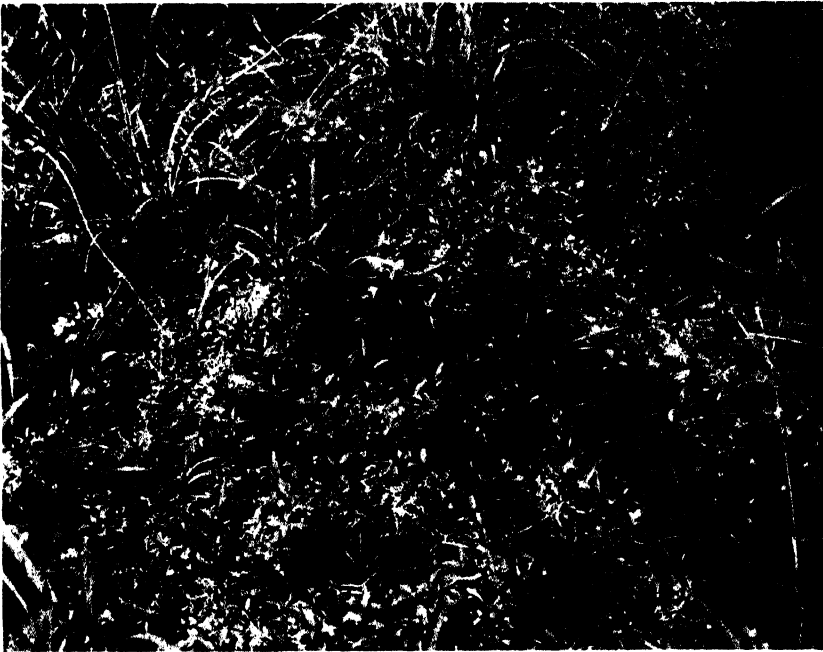


FIG. 19. Typical bare area in Carleton prairie due to death of little and big bluestem. Photo June 28, 1935.

lack of consolidation of the tufts into a dense sod showed that it had not been on the ground many years. Not infrequently extensive growths of blue grama grass or patches of buffalo grass formed an understory to the wheat grass. The seed crop of all three species was remarkably heavy. In other areas the short grasses formed alternes free of wheat grass as is typical of mixed prairie. This change in plant population had occurred within two or three years as a result of drought. The dead roots and rhizomes of the former bluestem dominants were everywhere, and in some places a few scattered living stems of big bluestem outlined or at least indicated the position of the former clumps. Drought had been so destructive that most of the wheat-grass area was no longer mixed but almost pure wheat grass.

Remaining bluestems.—In areas adjacent to wheat grass but on lower ground, the bluestems had not been routed and, indeed, little or no wheat grass was found. Locally, where drought had been least severe, big bluestem was frequently mixed on equal terms with little bluestem. Practically no bluegrass remained, but *Koeleria cristata* was common. Where great patches of ripened *Festuca octoflora* were found, much damage had been done. Here little bluestem was mostly dead and greatly injured big bluestem with half-dead bunches of *Bouteloua curtipendula* were found. Bunches of 20 to 50 stems of the fescue 18 to 20 inches tall were growing in the dead bunches of the bluestems. Extent of drought injury was often directly indicated by the density of stand of the fescue. Losses varied from 5 to 95 per cent on this nearly level, low ground. Frequently the little bluestem was entirely killed and the big bluestem, which made up 5 to 10 per cent of the cover, had not increased (fig. 20). Conversely, where big bluestem had been the most

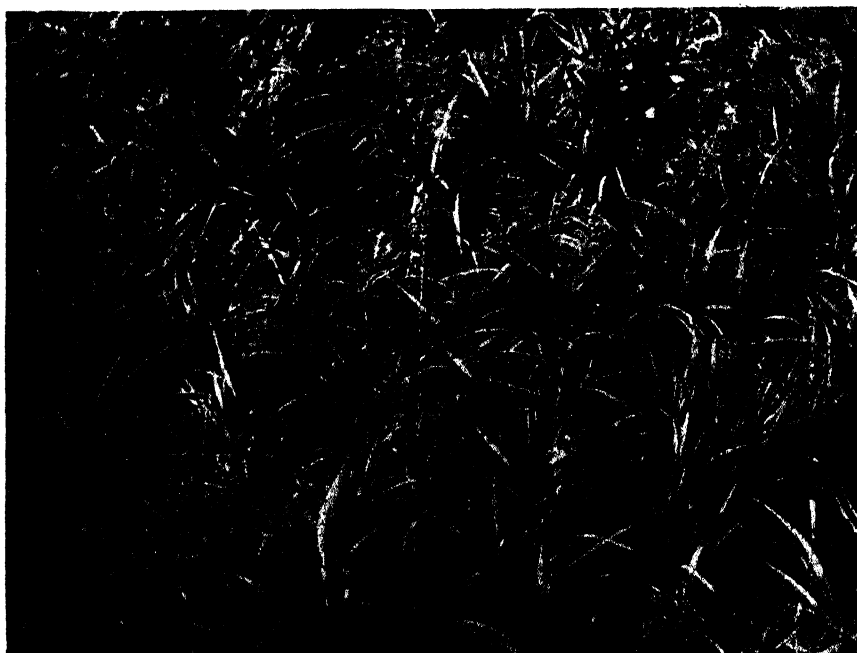


FIG. 20. An open cover of *Andropogon furcatus* resulting from the death by drought of the more shallowly rooted *A. scoparius* at Carleton, Nebraska.

important grass, the drought losses did not exceed 10 per cent. But commonly areas of 2 to 4 square feet, but of irregular shape, were bare of all vegetation. These may be reclaimed by big bluestem, but where both the former dominants had been killed, wheat grass had regularly invaded.

Mixed bluestems and wheat grass.—Over other large areas wheat grass had only partly claimed the prairie. Here it was mixed with 5 to 50 per cent or more of big bluestem, with the fragments of little bluestem that re-

mained, and with other prairie grasses and forbs. The alternes of grama grass were more numerous and much larger than before. Except for the short grasses, the lower layer of grasses and forbs was scarcely represented. Several species of only moderately deeply rooted forbs had nearly or entirely disappeared, while others with deeper root penetration had greatly increased.

Aster multiflorus had increased enormously, except in the least disturbed part of the prairie. Over considerable areas where drought had struck, but wheat grass had not invaded, it was practically the only species. The plants no longer formed bunches but a more or less uniform stand with rhizomes interwoven and hundreds of stems per square meter. It had claimed other areas in competition with the wheat grass.

Kuhnia glutinosa was prominent throughout except in the least disturbed parts. Its seedlings were abundant in many bare places as were also those of *Erigeron ramosus* and *Aster multiflorus*. *Rosa arkansana* was locally very prominent. *Amorpha canescens* remained green and was thriving although almost overwhelmed by the tall wheat grass. *Silene antirrhina* was common everywhere in bare areas but less so in the wheat grass. *Hedeoma hispida*, usually confined to short-grass alternes, was common to abundant everywhere. The lack of an abundance of Russian thistle, rough pigweed, etc., indicated an absence of accumulated drifts of dust.

The once uniform cover of vegetation presented an extremely disturbed, varied, and dynamic appearance. In the sea of drying wheat grass were revealed the islands of native bluestems, appearing at a distance little disturbed. Thinner stands of wheat grass indicated less drastic effects of drought, particularly on the big bluestem. The brown alternes of *Festuca* were strewn over the dead bodies of the former dominants while tangled patches of *Aster multiflorus* defaced similar scars of drought, but the land was made worthless. Which way the balance will swing in future years is dependent upon the amount of precipitation.

Nelson and Hebron prairies

A fine little bluestem prairie with one-third of the area shared equally with big bluestem lies near Nelson, Nebraska. It was in a thriving condition and free from invaders when studied in 1931.

By midsummer of 1935 half of the area had become covered with a layer of soil to a depth of about 0.5 inch. The native grasses had vanished. In their place *Bromus secalinus* (or a closely related species) and *Festuca octoflora* held complete possession except for a few deeply rooted native forbs, chiefly *Amorpha canescens*. Isolated alternes of wheat grass marked places where the wind-blown soil was about an inch deep.

Over the remaining half, *Festuca octoflora* and *Andropogon furcatus* were the chief grasses. *A. scoparius* was represented only by the merest remnants. Bare soil was everywhere, being clearly visible even at a distance. Although

big bluestem was sprinkled throughout, it was never consolidated except in the ravines where the stand was about one-half normal. Seedlings of *Koeleria* and *Poa* were common but there were no old plants. Dead rhizomes and bare soil declared the ravages of drought. Few or no interstitial species were found and few weeds had invaded. But for *Festuca*, the foliage cover, except on steep north banks, nowhere exceeded 30 per cent and frequently fell to 5 to 10 per cent. *Amorpha* and about eight other deeply rooted species composed the sparse societies.

At Hebron losses varied from 95 per cent on upper and middle slopes of south facing hills to 10 per cent near their foot. Elsewhere whole hillsides were covered with the dried, brown bunches of *Festuca octoflora*, or patches of *Erigeron ramosus*, alternates of wheat grass, and various weeds. The native perennial grass had been completely killed over many square rods and only relict patches remained in ravines and other favored places.

PRAIRIES OF SOUTHWESTERN IOWA

Study of a group of four prairies in southwestern Iowa, and two in southeastern Nebraska, none of which had been seriously if at all damaged, was made in 1935.

Glenwood and Corning prairies

Examination of prairies on the deep moist soils of the loess hills at Glenwood revealed that they had not been harmed by the drought. They were even better developed as regards height and density of foliage cover than at the previous examinations in 1931 and 1932.

Some drought effects were found in western Iowa on the glacial soils. An example is illustrated by the prairie at Corning, Iowa. This prairie covered hilltops, various slopes and valleys, as well as level uplands, and is typical of the rolling topography. The upland cover is of the well developed, little-bluestem sod-mat type except on the steepest slopes where the grass sometimes resorts to the bunch habit. Big bluestem occurs everywhere, shares equally the lower mesic slopes with little bluestem and forms fully 85 per cent of the cover on lower ground. Some alternates of *Sporobolus heterolepis* occur on the hill crests, while those of *Spartina michauxiana* with fringing *Elymus canadensis* and *Panicum* occupy the larger ravines.

The dry years had affected lowland vegetation by greatly decreasing the slough grass. In fact, with the lowering of the water table it had all but disappeared from the ravines and was replaced by *Agrostis palustris* and *Poa pratensis*. The stronghold of big bluestem in the lowlands had been somewhat weakened, the species being much more intermixed with little bluestem and other grasses.

The little-bluestem sod was scarcely disturbed on east and northerly slopes, but the loss on the uplands varied from 20 to 50 per cent. Other grasses such

as *Sorghastrum nutans*, *Sporobolus heterolepis*, *Poa pratensis*, *Andropogon furcatus*, and *Bouteloua curtipendula* were also considerably harmed. Many interstitials still remained, notably *Antennaria campestris*, rosettes of *Hieracium longipilum*, *Polygala alba*, young *Zizia aurea*, *Pedicularis canadensis*, and others. *Koeleria* was unusually abundant in these drought areas and *Aster multiflorus* had greatly increased along the driest ridge.

Anita and Oakland prairies

At Anita, Iowa, no traces of drought were in evidence. The tall, dense cover of vegetation with a wonderfully developed understory and an abundance of forbs overtopping the grasses was in striking contrast to the drought ravaged grasslands to the westward. Little bluestem was 18 inches tall on the driest slopes. Such species as *Fragaria virginiana*, *Antennaria campestris*, *Physalis lanceolata*, and *Zizia aurea*, as well as others which had not been able to endure the drought westward even on lowland, were here flourishing on the hilltops.

Similar conditions were found in a fine 40-acre prairie at Oakland, Iowa. The rank growth of grasses and forbs assured an unusually heavy yield of hay. At both stations sufficient rainfall had occurred to promote the usual excellent growth.

PRAIRIES AT AUBURN AND NEBRASKA CITY

At Auburn, in southeastern Nebraska, no harm had befallen the prairie probably because of timely local showers, although 20 miles northward at Nebraska City, considerable change had occurred. This prairie, fully described by Thornber ('01), has been intimately known by the writer since 1921 (Clements and Weaver, '24).

It is an area of 160 acres, much diversified in type. In ravines where *Elymus canadensis* formerly dominated, this species was much less abundant. *Spartina michauxiana*, which formerly covered a large tract of lowland, was in poor condition and much of its territory had been successfully invaded by *Panicum virgatum* and other less hydric species. This resulted from a general lowering of the water table.

In the extensive alternates of *Stipa spartea* the dead rhizomes of both of the bluestems, *Sorghastrum nutans*, and *Poa pratensis* were found everywhere. In fact little bluestem and bluegrass had practically disappeared as components of the *Stipa* vegetation. Many of the more shallowly rooted, younger bunches of *Stipa* had also died, but the excellent growth and widely spreading foliage of the current year obscured these losses. When the foliage was brushed aside, however, bare areas 1 to 3 or more square feet in extent were found in nearly every square meter. These bare areas, very irregular in outline, were practically continuous. *Stipa* had made such an excellent growth

that it appeared to dominate in much of the little-bluestem territory where its abundance in the basal cover was actually only 15 per cent. Outside the *Stipa* *altissima* losses of the bluestems and other grasses were far less. On midslopes they rarely exceeded 5 to 10 per cent but increased to 50 per cent locally. Careful measurements revealed that of this loss nearly four-fifths was that of little bluestem and bluegrass. The usual, widely spread weeds *viz.*, *Lepidium*, *Leptilon*, and *Silene* occurred, but not abundantly. *Erigeron* was unusually abundant but wheat grass was represented very locally in a few greatly disturbed places.

PRAIRIES IN NORTH CENTRAL KANSAS

A study of three tall-grass prairies was made just east of Mankato, Kansas, at Montrose, Belleville, and Haddam.

Montrose prairie

This prairie of 60 acres of moderately rolling land with some nearly level areas and shallow ravines, was examined in July, 1931, and again in June, 1932. "A large part is clothed with the *Andropogon scoparius* type with little bluestem furnishing 65 to 80 per cent or more of the plant cover. *A. furcatus* is present everywhere varying in importance from 5 to 20 per cent except on banks of ravines and in shallow draws where it usually takes complete possession. Hence there are considerable areas where big and little bluestem form a nearly equal mixture. *Sorghastrum nutans* ranks third in importance. It forms 3 to 5 per cent of the cover except on the long north slope which has been repeatedly burned. Here it replaces little bluestem in part and increases to 10 to 15 per cent. Bluegrass is often absent but usually ranges from 1 to 5 per cent in abundance. *A. furcatus* decreases to less than 10 per cent on south slopes, *Koeleria cristata* increases in abundance to 3 to 5 per cent, and *Bouteloua curtipendula* has holdings of 10 to 15 per cent between the bluestem bunches. Even spears of *Agropyron smithii* are seen and an occasional clump of *Bouteloua gracilis* and *Bulbilis dactyloides*. Forbs are abundant as regards species but the societies are not well developed."

Even casual examination late in June of 1935 showed that much damage had been done, and detailed examination revealed the nature of the destruction. Little bluestem had been injured most, in fact only mere remnants (about 1%) were left. Often big bluestem and slender grama remained where little bluestem had all died. Great mats of dead bunches and small clumps of grasses occurred everywhere. The basal cover was very open even on low ground, and the foliage cover did not exceed 50 per cent. In many places fully 75 per cent of the former vegetation had died, and often on flat hilltops big bluestem alone was left. The dead bases of the bluestems and other grasses were conspicuous everywhere. In several areas where

the scattered ruderal invaders were removed, only 1 per cent of the native grasses was alive. The rest was bare ground. Over the area as a whole the foliage cover (including invaders) was typically 25 to 30 per cent and the former basal cover of about 15 per cent had been reduced to 3 to 5 per cent. Even in the most favored situations losses of the bluestems were 10 to 20 per cent. Losses of the big bluestem were very severe; Indian grass suffered even more. A few good areas of big bluestem were found but these were local in or near the ravines. *Bouteloua curtipendula* had lost much ground. There was no *Stipa spartea*, and *Koeleria cristata* was represented only by seedlings. Bluegrass had been swept away, and the smaller interstitial panic grasses and forbs (except *Oxalis violacea*) were rare. Pro-



FIG. 21. Invasion of *Agropyron* into big-bluestem sod. The soil was washed away from this one-half square meter of sod revealing the dead underground parts of the former dominant (black) and the shining white rhizomes of wheat grass.

tection by the taller plants had failed and they had succumbed. Everywhere the soil was open to invaders.

Buffalo grass and blue grama grass had endured the drought well. The first especially was invading areas occupied by the bluestems and other less xeric grasses. They were thriving in the barest areas, growing in the old bunches of grasses as well as between them. Wheat grass had appeared in many places. Wherever soil had drifted in it occurred abundantly but it was also thriving in the barest areas (fig. 21). It was frequently intermixed with the short grasses. Many native forbs had almost or entirely disappeared and none had yet spread to such an extent as to constitute bad weeds. While the area was not weedy, there was an abundant potential weed population.

Salsola pestifer was common, *Helianthus annuus* was scattered throughout, and *Chenopodium album*, *Lepidium virginicum*, *Amaranthus retroflexus*, *Hordeum pusillum*, and *Solanum rostratum* occurred frequently.

Belleville prairie

This prairie, studied in midsummer of 1931, consists of about 30 acres with long east, west, and north slopes and a well developed broad ravine along the entire north side. The lowest part of the ravine bore a pure stand of *Spartina michauxiana*. About 5 acres supported an excellent stand of *Andropogon furcatus* with a little *Sorghastrum nutans*, and with intermixed *Panicum virgatum* and *Elymus canadensis* on the wetter margins. There was a good understory of *Poa pratensis*. A very localized zone of *Agropyron smithii* occurred in one portion. The higher land on all slopes was dominated by *Andropogon scoparius* with about 15 per cent of *Koeleria cristata* and a good admixture of *A. furcatus*. The steep portions of the hills showed locally almost pure alternes of *Bulbilis dactyloides* and *Bouteloua gracilis* with bunches of *Sporobolus asper*, *Opuntia* spp., *Plantago purshii*, and *Hedeoma hispida*. About these, as well as throughout the bluestem sod, *Bouteloua curtipendula* was well distributed.

By 1935 the small wheat-grass alterne had developed into a large one 2 to 3 rods wide and 10 rods long. Dust had covered most of the lowland 0.5 to 1 inch deep and nine-tenths of the bluestem area was occupied by a nearly pure stand of wheat grass. The slough-grass area was much less extensive and had been replaced in part by *Panicum virgatum* and *Elymus canadensis*. Some bluegrass still persisted. A dust cover of even an inch was very detrimental to the bluestem. Where dust blew from the hillside and did not lodge immediately next to the bank, the uncovered area was still occupied by big bluestem. Otherwise the banks too were sodded over with wheat grass. Nearly all low-growing forbs were absent.

Where much dust was deposited on the uplands, an open stand of wheat grass prevailed with only relicts of former grasses. Here the basal cover usually did not exceed 2 per cent. Little bluestem was all dead on the west-facing slope, and only traces remained on the east one. Big bluestem was represented by the merest relicts. In fact, fully 95 per cent of the original tall grass had died; where most sheltered, scarcely 25 per cent remained. There was no *Sorghastrum*, only a little *Bouteloua curtipendula*, and small amounts of *Koeleria*. Many plants of *Opuntia humifusa* had died and decayed.

Although both blue grama grass and buffalo grass had suffered considerable losses, as shown by marked thinning of the stand, both were rapidly recovering. They still held their former areas and buffalo grass especially was spreading rapidly. New centers were being established over the slopes. *Aster multiflorus*, only 8 to 12 inches tall, formed great patches and was rapidly reclaiming the bared land. *Spermolepis divaricata* had spread widely.

Great bare areas were everywhere and erosion by wind and water was imminent. Plants of the understory had disappeared. Weeds populated the soil thinly in places, elsewhere they grew thickly. The chief invaders were

Bromus secalinus and *Festuca octoflora*, both in extensive alternes (figs. 22 and 23). Other weeds of much importance were *Silene antirrhina*, *Lepidium virginicum*, *Hordeum pusillum*, *B. tectorum*, *Plantago purshii*, and *Chenopodium album*.



FIG. 22. Alternes of *Bromus secalinus* (light colored) in prairie badly depleted by drought near Haddam, Kansas. July 1, 1935.

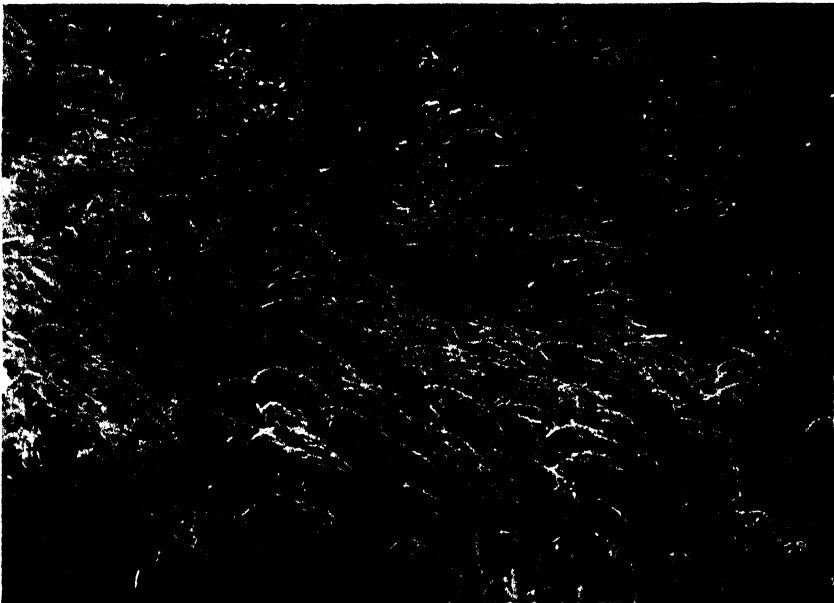


FIG. 23. Dense stand of *Festuca octoflora* in prairie near Belleville, Kansas, in ground formerly occupied by little bluestem.

Haddam prairie

Only about 8 acres of a 40-acre prairie near Haddam, Kansas, remained largely intact. It had the double advantage of the protection of a dense hedge of untrimmed *Maclura pomifera* and a north slope exposure. Even here there was 20 to 50 per cent loss. Over the remainder, the bluestems had met losses of 60 to 100 per cent, about 15 per cent of the original grass cover remaining. The usual alternates of brome grass and wheat grass were extensive. *Aster multiflorus* and *Spermolepis divaricata* formed dense weedy patches, and practically all of the ruderals of other prairies were also found here.

LOSS OF INTERSTITIALS

With the wilting of the layer of grasses on uplands and their death over great areas, plants of the ground layer were not afforded the usual protection from insolation at this most critical time of great drought. Consequently most of the understory species suffered great losses and in the drier, western prairies practically all succumbed. This change was impressive.

Antennaria campestris, one of the seven most important prairie forbs, was all but swept away from the more western prairies and suffered enormous losses elsewhere. The fibrous roots apparently do not penetrate very deeply. The plants made some gains in 1935, but by midsummer new shoots, like those of shallow-rooted seedlings, began to wilt as water in the surface layers of soil again became exhausted.

Poa pratensis was almost completely killed except in a very few usually wet spots in the westernmost prairies. Eastward it died on hilltops and exposed slopes and even on lower ones where the old debris had been removed by fire. In many nearly level prairies it remained only in the bottom of ravines.

Panicum scribnerianum, *P. wilcoxianum*, and other low-growing panic grasses were affected to an extent similar to that of bluegrass. During 1935 they were rarely found. Other interstitial grasses somewhat similarly affected were *Agrostis hyemalis* and *Eragrostis pectinacea*.

In general the basal cover was reduced somewhat in proportion to the death of the tall grasses. *Anemone cylindrica* and rosettes of *Hieracium longipilum* practically disappeared. *Fragaria virginiana*, *Viola pedatifida*, *V. papilionacea*, *Antennaria plantaginifolia*, *Senecio plattensis*, species of *Polygala*, *Sisyrinchium*, and *Physalis* are further examples of plants that suffered especially from the drought. *Galium tinctorium* and *Anemone canadensis* as well as many others were greatly depleted or failed to grow on low ground.

Among taller plants, *Equisetum laevigatum* and *Toxicodendron rydbergii* were greatly injured or killed.

INCREASE IN NATIVE GRASSES

Agropyron smithii made the greatest increase of any native grass. Formerly it occurred only sparingly in the eastern prairies and was confined mostly to the thinner soils and especially to roadsides, alkali spots, or greatly disturbed places. It is now widely established along roadsides, especially where disturbance such as dust accumulation has occurred. Entrenched at least in small areas in practically all of the disturbed prairies and taking possession of extensive areas in others, especially westward, it has caused profound change. It thrives in places where the bluestems have died, promptly reclaims areas overwhelmed by dust, and from these vantage points has rapidly extended its territory during the years of drought. Only deeply rooted forbs remain in the dense sod of this tall grass. Its vigorous growth in early spring and its migration by long, slender rhizomes are distinct assets.

Bulbilis dactyloides, profiting by the death of its tall competitors, is increasing its holdings, often very vigorously, in grasslands bordering the mixed prairie. *Bouteloua gracilis* is behaving similarly although its invasion is much slower. It is also locally common on the steepest upper slopes in the center of the area. It was almost unharmed in the same square meters where all of the little bluestem died.

Festuca octoflora has become abundant in the bare areas of the eastern Nebraska prairies. Westward its abundance has increased until it is locally in complete possession of hilltops and slopes where the dominant grasses have died. Bunches of 20 to 30 stems of this annual growing out of the dead crown of little bluestem were found regularly. In a single square meter, 200 bunches were not uncommon. The abundant and very light seed ripens in July and is broadcast by the wind.

INVASION BY NATIVE FORBS

Aster multiflorus has become a bad weed in many of the prairies throughout the area, but not in all, being almost absent in some that were greatly disturbed. It ranged from great local abundance to complete temporary control over one-fifth to one-half of certain large prairies. The thick stand of somewhat woody, tangled stems, 18 to 26 inches tall, formed almost thicket-like growths.

Erigeron ramosus has become a bad weed in about half of the drought-damaged prairies. This annual seeded so thickly that frequently 20 to 30 plants per square decimeter clothed the bare soil where the grasses had died. Height varied from 12 to 30 inches. Extensive societies, distinguishable at long distances, were common.

The catchfly, *Silene antirrhina*, usually not at all abundant in prairie, was one of the five most important, weedy native forbs. It was found in all but a few of the most westerly prairies. In the bared areas the plants occurred in large numbers and often reached more than twice their usual stature. Like

the following, this annual dried in June. The slightly roughened, nearly spherical seeds, are one-half millimeter or less in diameter and appear as specks of dust.

Specularia perfoliata became extremely abundant in the eastern half of the area. Plants were often grouped in large numbers and grew and branched in an unusually vigorous manner. The seeds are very minute, flat, disk-shaped bodies, appearing like small specks of dust. They are produced in great abundance and easily carried by wind.

Many bulbous plants such as *Allium mutabile*, *Erythronium mesochoreum*, and *Anemone caroliniana* occurred in unusual abundance and flourished during 1935. Of greatest abundance among these was *Oxalis violacea*. It was found commonly to very abundantly in most of the drought-injured prairies, often occurring in great abundance in areas where the dead grass left the soil bare. *Hedeoma hispida* and *Plantago purshii* were scattered more or less abundantly over the bared and semibared areas in nearly all of the prairies. Formerly they were found nearly always in association with the short grasses only. The seeds of *Hedeoma* are small, light and readily distributed by the wind.

Other forbs that were of unusual local abundance in a few of the prairies were *Artemisia gnaphalodes*, *Solidago glaberrima*, *Gaura parviflora*, and *Achillea occidentalis*. They were sometimes practically the only species surviving over considerable tracts.

SEEDLINGS

Careful note of the chief seedlings of prairie plants was made during 1935. Seedlings of *Erigeron ramosus* were by far the most abundant, easily exceeding those of all other species combined. By the beginning of the summer drought they were 6 to 7 inches tall. Seedlings of *Koeleria cristata* ranked second, with an abundance of those of *Aster multiflorus*, *Kuhnia glutinosa*, and various goldenrods, in order. Those of legumes such as *Amorpha canescens*, *Astragalus crassicaupus*, and *Psoralea floribunda* were much less common. The dry spring had been unfavorable to early seed germination, but after May 15 moisture was plentiful.

INVASION BY RUDERALS

Certain ruderals, normally not found in prairies, were widely distributed. *Lepidium virginicum* was common to abundant throughout nearly all of the prairies where death by drought resulted in enough light for ecesis. This weed was often a fairly good indicator of the amount of bared space. Seeds were borne in such abundance that they literally covered the soil beneath densely aggregated plants. They are flat, about a millimeter long, slightly less in width, and easily carried by the wind. Peppergrass was found widely distributed in 1935 from the Missouri River to the Rocky Mountains of Colorado and far into Wyoming.

Leptilon canadense was common to abundant in the prairies of the eastern half of the area and in some more westerly ones. The plants were frequently 2.5 to 3.5 feet tall. In pastures they formed veritable thickets which greatly delayed one's progress.

Bromus secalinus occurred in very great abundance in the western part of the area where it frequently covered hillsides in the drought-stricken prairies. *Bromus tectorum* also occurred in moderate amounts but mostly eastward.

Tragopogon pratensis varied from great abundance (fig. 7) to widely scattered plants, occurring most abundantly eastward. *Salsola pestifer*, conversely, was confined largely to the western part. *Helianthus annuus*, *Solanum rostratum*, and *Hordeum pusillum* were also common to abundant weeds in prairies westward. *Amaranthus retroflexus* and *Lactuca scariola* were usually more abundant in the eastern Nebraska prairies.

Studies in the Mixed Prairie

Studies of the environmental factors and the structure of the mixed prairie of west-central Kansas were begun before the advent of the great drought. They were continued until the end of 1935. Intensive investigations have been pursued in a tract of 750 acres of unbroken prairie belonging to the Fort Hays Kansas State College. The exclosures, instrument stations, etc., were located about 2.5 miles west of Hays. These prairies cover a rolling topography adjacent to the valley of Big Creek, a branch of the Smoky Hill River. The elevation is about 2,100 feet, the level hilltops rising about 200 feet above the valley floor.

TYPES OF VEGETATION

Three general types of vegetation are common, with varying degrees of intermixtures. The most extensive is the little-bluestem type which occupies the hillsides and extends across shallow ravines. It extends over the brows of the hills and far beyond where the slopes continue, but gives way more or less abruptly to short grasses on the level uplands (fig. 24). The big-bluestem type is much more limited in extent. It occupies the deeper ravines, lower portions of gentle slopes, and well watered lowlands. The short-grass type is found widely distributed over the nearly level uplands. Smaller areas and strips also occur at the bases of hills, especially on south-facing slopes, where the soil is underlaid with an impervious clay.

Numerous grasses beside the dominant are found regularly in the little-bluestem areas. *Andropogon furcatus*, *Panicum virgatum*, and *Bouteloua curtipendula* extend far up the hillsides. They are more or less replaced in drier situations near the brows of the hills by *Sporobolus pilosus*, *Bouteloua hirsuta*, and *B. gracilis*. Distribution of the little-bluestem type is largely controlled by the shallow soil above the underlying limestone. On the nearly

level uplands, where a mature soil profile has developed, it is replaced by the short-grass type. On the lowlands, where deep alluvial soil is moistened by run-in water, little bluestem is replaced by the taller grasses.

Chief associates of the big bluestem are *Bouteloua curtipendula*, *Agropyron smithii*, and *Sporobolus asper hookeri* with smaller amounts of *Panicum virgatum*, *Elymus virginicus*, *E. canadensis*, *Sorghastrum nutans*, and *Carex grvida*.

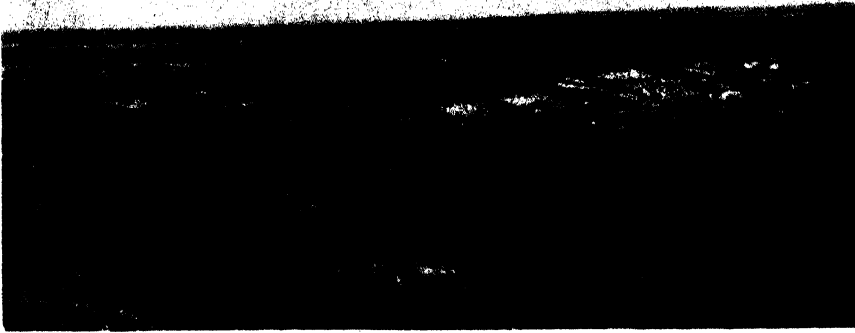


FIG. 24. General view of the mixed prairie near Hays, Kansas. The *Andropogon scoparius* type, which covers the slopes and occurs on the limestone outcrops, gives way on the level uplands (foreground and upper left) to the *Bulbilis-Bouteloua* type of vegetation.

The *Bulbilis dactyloides-Bouteloua gracilis* type is characterized by a predominance of buffalo grass, by blue grama grass in probably about one-third as great abundance, and by bunches of wire grass, *Aristida purpurea*, and little bluestem. The bunch grasses may occur as widely scattered plants, but increase in numbers with a more favorable water supply. *Sitanion elymoides* is a common species of much less importance.

PRECIPITATION

The mean annual precipitation at Hays over a period of 68 years is 22.84 inches. The highest mean monthly rainfall of 3 to 3.5 inches occurs during May, June, July, and August. The dry years of 1933 to 1935 inclusive, with an average of only 15.46 inches precipitation, were preceded by 6 years (1927-32) when the mean annual precipitation of 27.76 inches was 4.92 inches above the 68-year average. Average precipitation by months during the 68-year period, the wet period, and the drought are shown in figure 25. Data for the first two periods were supplied by Mr. A. L. Hallsted from the Fort Hays Kansas Experiment Station; that for the dry period was obtained at the prairie station 2.5 miles west of Fort Hays and 200 feet above the valley

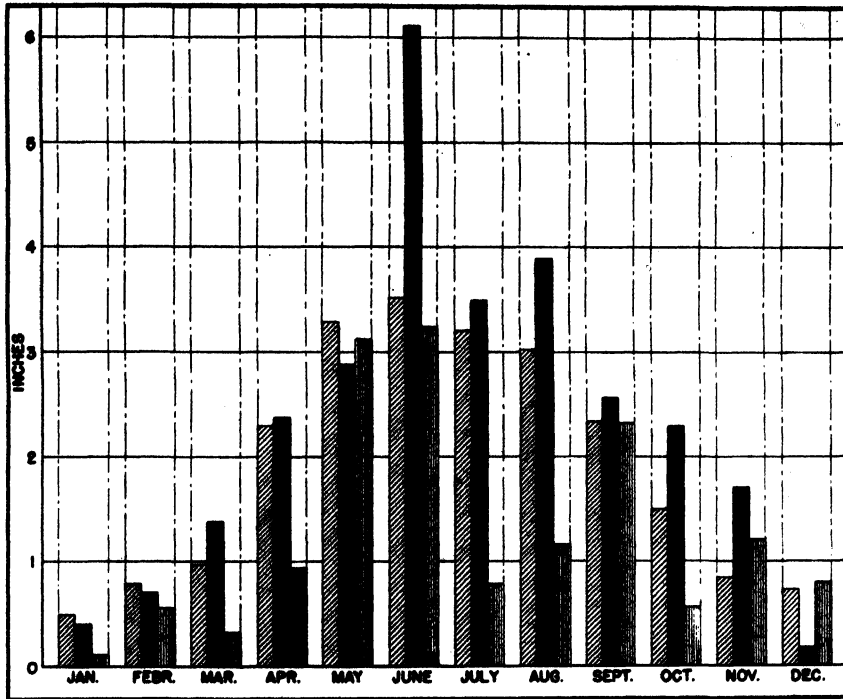


FIG. 25. Average precipitation by months at Hays, Kansas, over a period of 68 years (left hatch), from 1927 to 1932 inclusive (black), and from 1933 to 1935 inclusive (vertical hatch).

of Big Creek where the government rain gauge is located. A standard rain gauge was maintained at a height of 3 feet, and readings were taken after each shower. Precipitation by months during the three critical years is shown in table I.

TABLE I. *Precipitation by months during the drought*

Yr.	J.	F.	M.	A.	M.	J.	Jl.	A.	S.	O.	N.	D.	T.
1933	.07	.21	.33	2.14	2.53	.56	1.70	1.17	2.03	.03	.54	2.17	13.48
1934	.29	1.16	.45	.37	1.55	3.95	.67	2.21	1.59	.70	.75	.02	13.71
1935	T	.30	.15	.21	5.26	5.12	.01	1.30	3.35	.95	2.35	.20	19.20

Precipitation for 1933 totaled only 13.48 inches which was 9.36 inches below normal and 14.28 inches less than that of the favorable period just preceding. A moist spring was followed by drought in June and low rainfall during the hot summer. Conditions resulting from a very dry autumn were somewhat ameliorated by 2 inches of precipitation in December.

The spring of 1934 was extremely dry. The 1.55 inches rainfall in May was dissipated in 8 showers, only one of which exceeded .31 inch. The 3.95 inches in June included 4 rains of .42 to 1.49 inches. The 6 remaining showers were so small and widely scattered as to have practically no effect upon soil

moisture. July had only 2 showers, .15 and .52 inch. August with 2.21 inches had only one rainy period when any but the surface inch or two of soil was moist. This was at the end of the month when 1.35 inches of water fell during a period of two days. Six widely scattered showers, none exceeding .38 inch, fell in September and netted 1.59 inches of moisture. Scattered showers in October and November totaled .70 and .75 inch, respectively. The winter was extremely dry. No precipitation fell in December. The total for the year was only 13.71 inches.

January of 1935 had no precipitation. The highest precipitation, .30 inch, of the following three months occurred in February. It had no effect upon replenishing soil moisture. Thus from October 18, 1934, to May 11, 1935, there was no efficient precipitation. The drought was broken by good, well distributed showers beginning on May 11 and extending to June 28. The total precipitation for May was 5.26 inches, and June had 5.12 inches. No rain fell during July. Of the 5 showers in August (total 1.3 inches) only one, .52 on August 20, moistened the surface inches of parched soil. Thus seven weeks of excellent conditions for growth were followed by seven weeks of

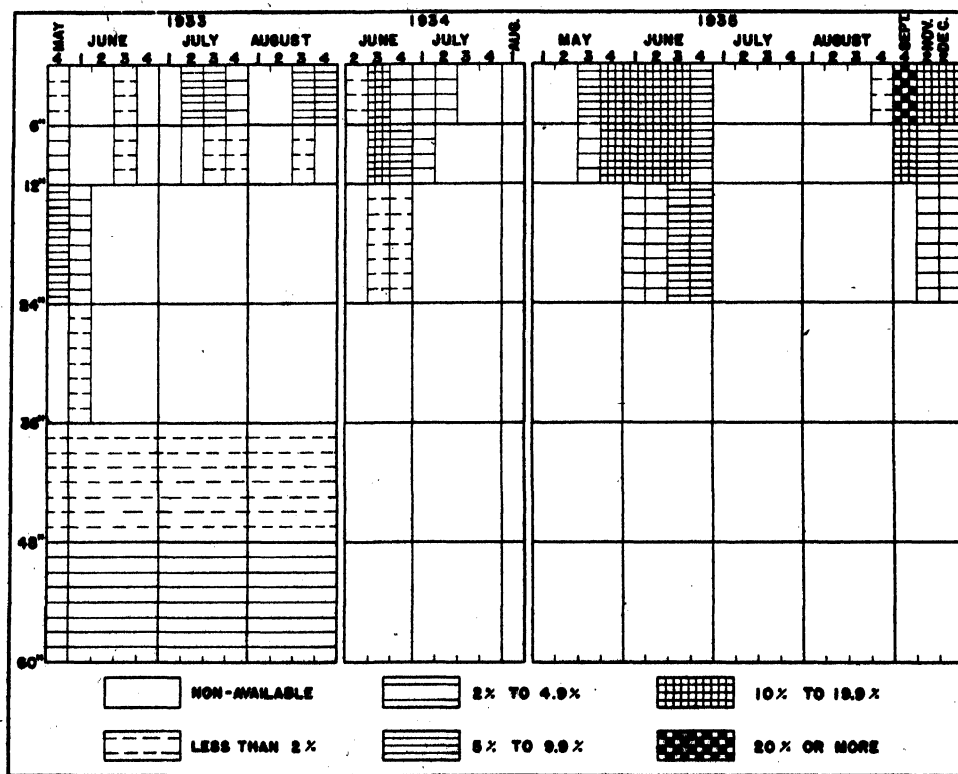


FIG. 26. Available water content of soil in the short-grass type at Hays, Kansas, at the several depths to 5 feet, during 1933 to 1935. The hygroscopic coefficient of the soil was considered as the approximate percentage of nonavailable water for the depth at which the sample was taken.

drought. On September 8, .95 inch of rain fell, and 2.4 inches on September 26, furnishing a total rainfall of 3.35 inches for the month. The fall and early winter months were moderately moist and some moisture accumulated in the surface soil. Precipitation for the year was 19.2 inches.

WATER CONTENT OF SOIL

The soil moisture relations have been determined during 2 to 3 years in each of the three types of vegetation. Duplicate samples in the short-grass and big-bluestem types were taken regularly to a depth of 5 feet. Owing to the presence of underlying limestone, sampling with the geotome in the little-bluestem type was confined to 2 feet in depth. Samples in the soil pockets between the rocks were also taken, but irregularly.

Water relations in the short-grass soils are shown in figure 26. Here it may be seen that following a moist spring the June drought resulted in complete exhaustion of water available for growth from 1 to 3 feet. Although

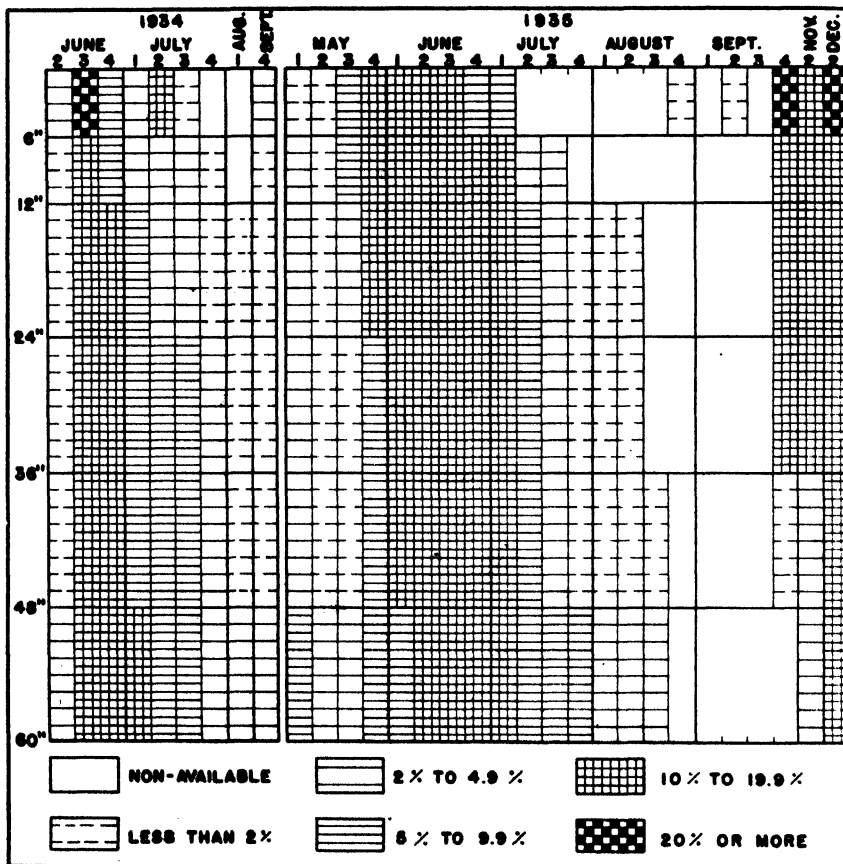


FIG. 27. Available water content of soil in the big-bluestem type at Hays, Kansas at the several depths to 5 feet, during 1934 and 1935.

the deeper subsoil remained moist (1 to 5 per cent), only intermittently was water available in the surface foot. By the second week of the following June water was nonavailable at any depth except in the surface 6 inches. Then the surface foot of soil was supplied with a low water-content during 3 to 4 weeks and the second foot for only 2 weeks. The subsoil remained dry. During 1935 the soil was moist from the third week in May until the first of

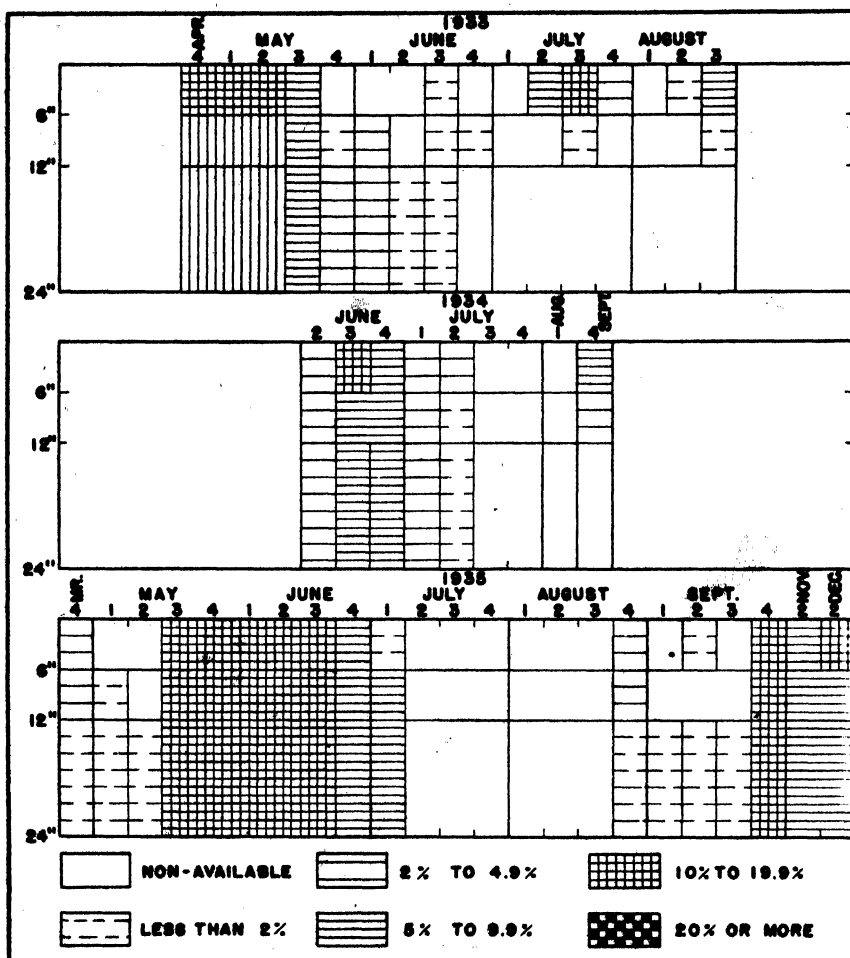


FIG. 28. Available water content of soil in the little-bluestem type at Hays, Kansas, to the underlying rock at a depth of two feet.

July. No soil moisture was available during July and practically none in August. Rains in September and later moistened the surface two feet.

In the lowland, big-bluestem habitat, soil moisture was available, although at some periods in small amounts, during the entire growing season of 1934 and until late in July of 1935 (fig. 27). An exception was nonavailable water in the first foot during late July and early August of 1934. Beginning with the second week of July, 1935, water became deficient in the surface 6 inches,

and two weeks later this condition extended to a depth of one foot. After two more weeks no water was available to 3 feet in depth. A week later water became nonavailable at all depths, except that intermittently local showers moistened the surface. This condition continued until the last week of September, after which rains replenished both surface and subsoil moisture to a depth of 5 feet.

A fairly close relation was found between rainfall and available soil moisture of the first 2 feet in the little-bluestem type (fig. 28). Extensive studies of root distribution revealed that little bluestem drew upon soil moisture stored in the pockets and crevices of the rocks to a depth of 3 feet but big bluestem to a depth of 4 to 5 feet.

TEMPERATURE AND HUMIDITY

Thermograph records of air temperature at a height of 4 inches above the soil surface and soil temperature at a depth of 3 inches, both in the short-grass area, were obtained. These data are averaged by weeks in figure 29. During the most severe period of the 1934 drought (June 25 to August 20), the average daily maximum temperature ranged between 96° and 111° F. The aver-

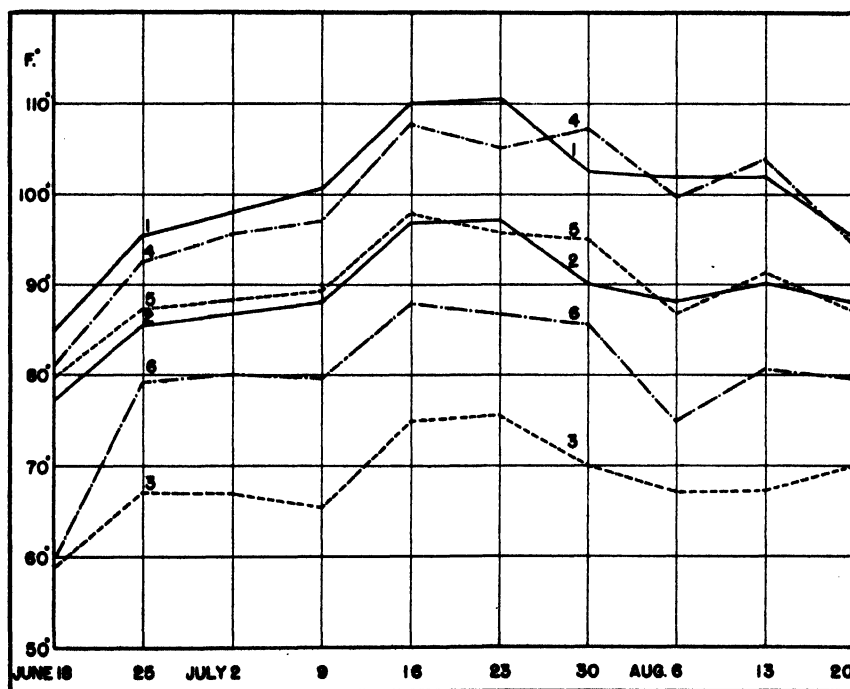


FIG. 29. Temperatures of air and soil by weeks at Hays, Kansas, during 1934. 1, Average daily maximum temperature; 2, average day temperature (6 A.M. to 8 P.M.); 3, average daily minimum temperature; 4, average daily maximum soil temperature at 3-inches depth; 5, average daily soil temperature; and 6, average daily minimum soil temperature.

age day temperature varied from 86° to 97° F., and even average daily minimum temperatures were 66° to 76° F. Although these temperatures were no higher than those experienced in the tall-grass prairie at Lincoln (Weaver, *et al.*, '35), the period of intensive heat was about two weeks longer.

Average daily maximum soil temperatures were at first slightly less than those of the air, but finally exceeded those of air temperature. Likewise, average day temperatures of soil and air did not depart widely, and average daily minimum soil temperatures were regularly 8° to 14° F. higher than those of the air.

The humidity regularly fell to 25 to 15 per cent during the afternoons, and often to 11 per cent or less. Since grasses in phytometer cans that were watered, as well as watered plants in experimental plots did not die, it is believed that the great loss of vegetation was due to drought and not directly to high temperatures. Increased temperature decreases the relative humidity which results in increasing water losses by transpiration as well as by evaporation from the surface soil. It is usual for high temperatures and drought to work together in the destruction of vegetation, but drought is usually the direct cause of death.

EVAPORATION AND WATER LOSS FROM VEGETATION

Average daily water losses by weeks from pairs of standardized, white, spherical atmometers ranged during this period of stress from 76 to 138 cc. These losses were 1.5 to 1.7 times as great as those recorded during this period in the tall-grass prairie at Lincoln.

Losses of water through transpiration and surface soil evaporation from large sod phytometers sunk 1.5 feet in the soil, each lot in its own habitat, were very high. The short grasses lost 12.2 and 8.3 pounds per square foot per week, the little bluestem 13.9 and 10.4 pounds, and the big bluestem 11.8 to 11.3 pounds per week during the third and fourth weeks in July, respectively. Losses from the little bluestem were 11 per cent greater than from similar unit areas at Lincoln.

THE 1935 DROUGHT

Brief note of environmental conditions during 1935 is necessary in order that the excellent early growth, followed by severe wilting and frequently by death of the vegetation, may be understood. A series of the worst dust storms in the history of Kansas occurred during the late winter and spring of 1935 (fig. 30). Hot, desiccating winds of high velocity occurred commonly during the summer. The moderate temperatures of spring and early summer were followed by average daily maximum air temperatures of 98° to 104° F. during the almost rainless months of July and August. Soil temperatures likewise reached nearly 100° F. Average day humidity decreased rapidly from 74 to 78 per cent in June to 44 to 57 per cent. From the middle

of July to August 20, average daily minimum humidity ranged between 21 and 29 per cent. Average daily evaporation losses by weeks increased from the 12 to 30 cc. losses of June, to 65 to 83 cc. during this period of heat and drought. Losses of water from phytometers were very high.

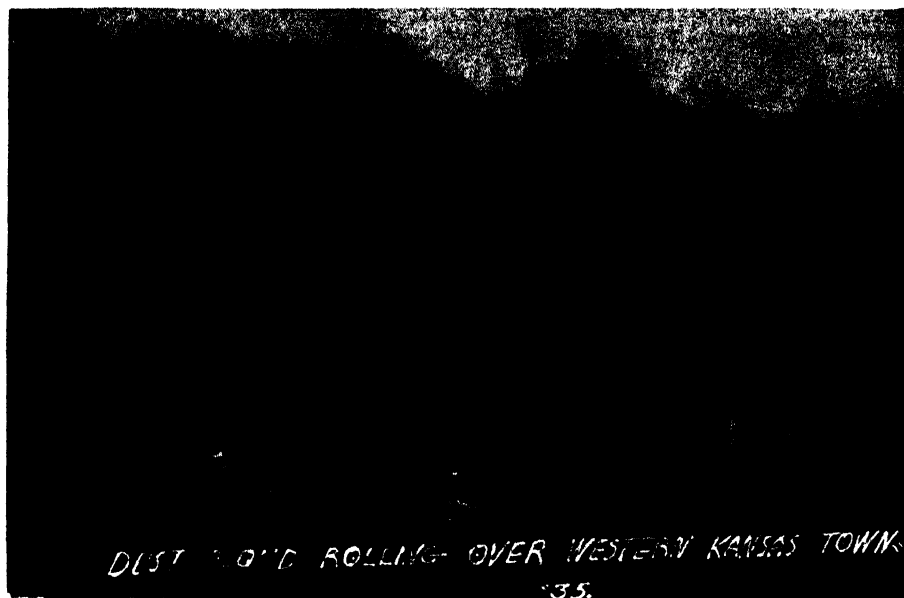


FIG. 30. Dust cloud rolling over a west-central Kansas town. Photo by Potter, Ness City, Kansas.

EFFECT UPON THE VEGETATION

The changes in the cover of vegetation have been studied intensively by means of over 160 permanently established quadrats as well as by continued observation and estimates over the whole area. A very few of these quadrats, selected to show some of the various general trends in the several communities, are presented, each with a brief description of the change (figs. 31-43).

In making the quadrats, the pantograph-chart method has been employed. The short grasses and open sod of the little-bluestem type lend themselves readily to this method of study (cf. Savage, '34). The ground or basal cover represents that portion of the soil occupied by the basal cross section of the crowns, prostrate stems, and by stolons of living plants. Where such plant parts were less than one centimeter distant, the area was considered as being fully occupied. Each chart had an area of 2.25 sq. dm., or a ratio to the length of the quadrat of 1 to 6.66. The percentage of basal cover, percentage of the cover constituted by the various species, etc., were determined from the charts by means of planimeters.

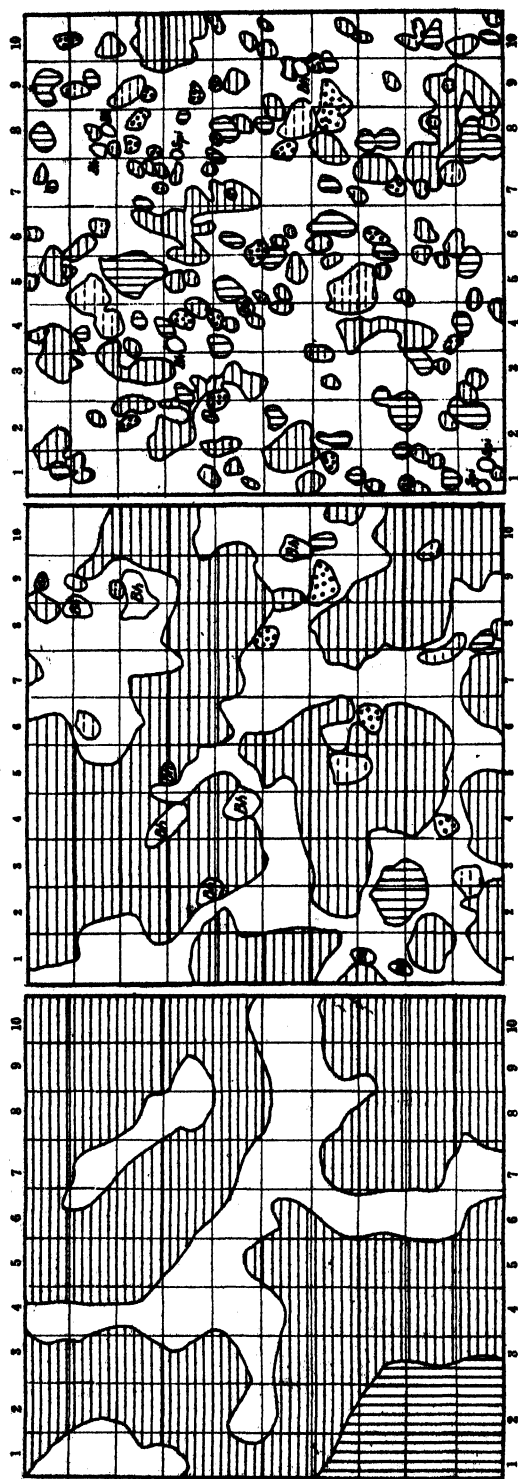


FIG. 31. Quadrat in ungrazed, typical little-bluestem type on hillside, charted in October of 1932 (left), 1934 (center), and 1935 (right). The limestone lies 8 to 15 inches below the soil surface but the roots penetrate into the rock crevices to depths of 2.5 to 4 feet. Note the great decrease in *Andropogon scoparius* especially during 1935, and the accompanying increase in bare soil. During 1934 the bluestem existed upon the reserve water supply in the soil pockets, cracks, etc., in the rock. *Spi. Sporobolus pilosus*.

Species, etc.	Composition of basal cover in per cent		
	'32	'34	'35
<i>Andropogon scoparius</i> (horizontal hatch)	67.5	51.7	14.4
Bare ground (unmarked)	24.8	42.5	74.0
<i>Andropogon furcatus</i> (vertical hatch)	7.7	1.5	7.7
<i>Bouteloua gracilis</i> (dotted)	0.0	1.2	2.8
<i>Bouteloua hirsuta</i> (Bh)	0.0	1.1	0.5
<i>Bouteloua curtipendula</i> (broken horizontal hatch)	0.0	2.0	0.6

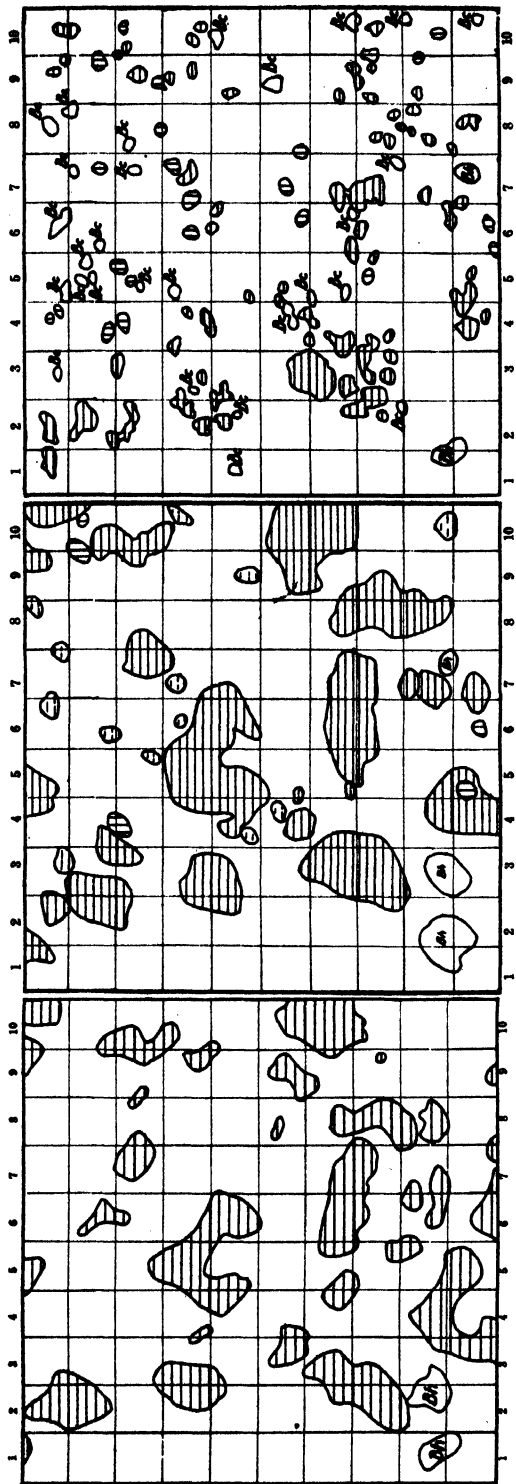


FIG. 32. Quadrat typical of the open little-bluestem type on thin soil near the crest of a hill. This ungrazed area was charted in the fall of 1932 (left), 1934, and 1935 (right). Limestone rock outcropped at the soil surface. Basal cover of *Andropogon scoparius* (horizontal hatch) remained about the same, 19.4 and 21.3 per cent, until 1935, when it decreased to 6.4 per cent. *Bouteloua hirsuta* (Bh) changed from .8 through 1.5 to .4 per cent. *Andropogon furcatus* (vertical hatch) increased from .6 per cent ('34) to 1.5 per cent ('35), and *Bouteloua curtipendula* (Bc) in 1935 was 1.6 per cent. The persistence of little bluestem and the gain of hairy grama during 1934 were probably due to an excess of water stored in the soil pockets of clay in the decomposed limestone. The entrance of big bluestem after 1932 is in agreement with the general findings that it gained ground elsewhere at the expense of the more shallowly rooted little bluestem. Note the open character of the vegetation and the great losses sustained during 1935.

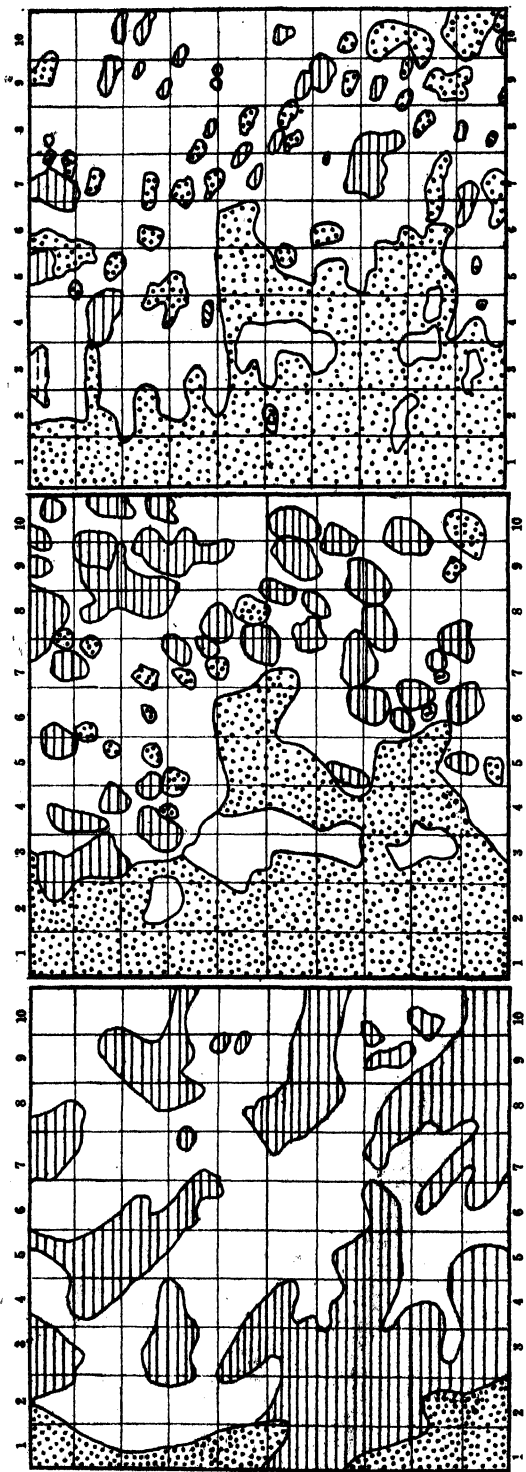


FIG. 33. Quadrat in ungrazed little-bluestem type farther over the crest of a hill and farther up the gentle slope than the preceding. It lies on the ecotone between tall grass and short grass (fig. 44). The rock lies about two feet below the surface. During wet years little bluestem tends to extend outward into the short grasses. During 1932 (left) little bluestem (horizontal hatch) occupied 39.4 per cent of the area but decreased to 16.3 per cent in 1934 and to 4.5 per cent in 1935. Short grasses (dots) increased from 7.2 to 33.7 per cent in 1934 and to 37.7 in 1935. *Arisida purpurea*, *Bouteloua curtipendula*, and *Cirsium undulatum* appeared in 1935. The invasion of the short grasses into the bordering area of bluestem occurred along all ecotones where the rocky soil was sufficiently deep for good development of the short, sod-forming grasses. The large amount of bare ground, 53.4 per cent in 1932, is characteristic of this type.

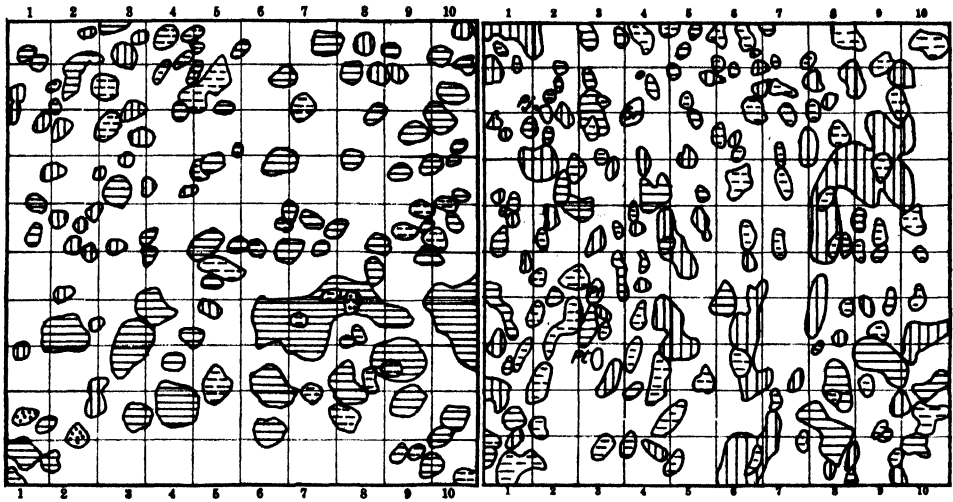


FIG. 34. Shift in grass populations in typical little-bluestem type, with a good mixture of big bluestem, as a result of drought. The local area was protected from grazing. There was some run-in water and rapid percolation among the rocks. First charting (left) in October, 1934, and second in October, 1935. Little bluestem (horizontal hatch) decreased from 17.8 to 7.6 per cent. Big bluestem (vertical hatch) increased from 3.7 to 14 per cent. Slender grama (broken horizontal hatch) increased from 5.1 to 11 per cent, but the traces of blue grama (dots) entirely disappeared. Forbs were not charted. Throughout the whole little-bluestem type, big bluestem showed smaller losses from drought than did little bluestem, and often increased at the expense of the latter as a result of its deeper root system.

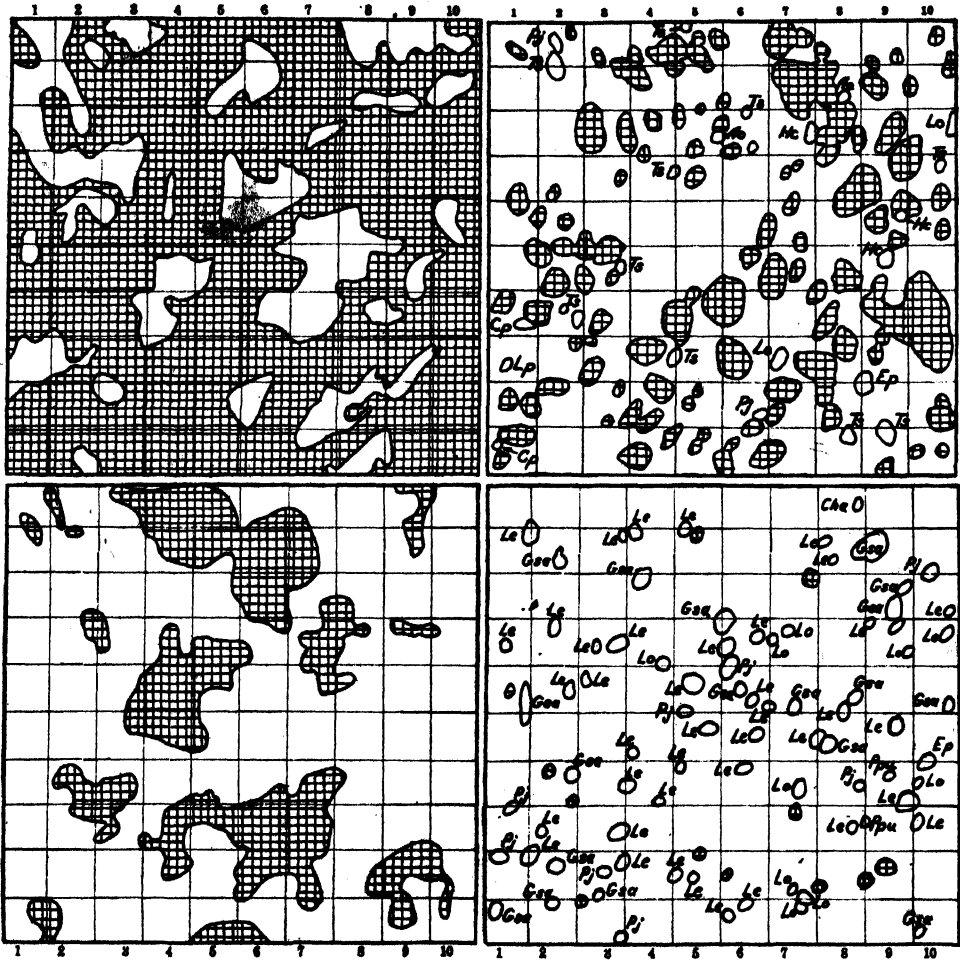


FIG. 35. Quadrat (above) in little-bluestem type on a north-facing slope in overgrazed pasture 16 miles north of Hays, Kansas. Total ground cover was 74.6 per cent (left) and total living cover was 27.1 per cent (right) in the fall of 1935. The forbs constituted only 2.1 per cent of the latter. Chief among these were *Tetraneuris stenophylla* (Ts) and *Hymenopappus corymbosus* (Hc). The ground cover was reduced 47.5 per cent during 1935. Quadrat (below), the same, except it is on a south-facing slope. The total ground cover of tall grasses (left) was 22 per cent of which only traces (.8 per cent) remained alive in late fall. The forbs *Leucelene ericoides* (Le), *Gutierrezia sarothrae* (Gsa), *Lesquerella ovalifolia* (Lo), and others formed a cover of 8.3 per cent. Total loss of ground cover was 12.9 per cent during 1935.

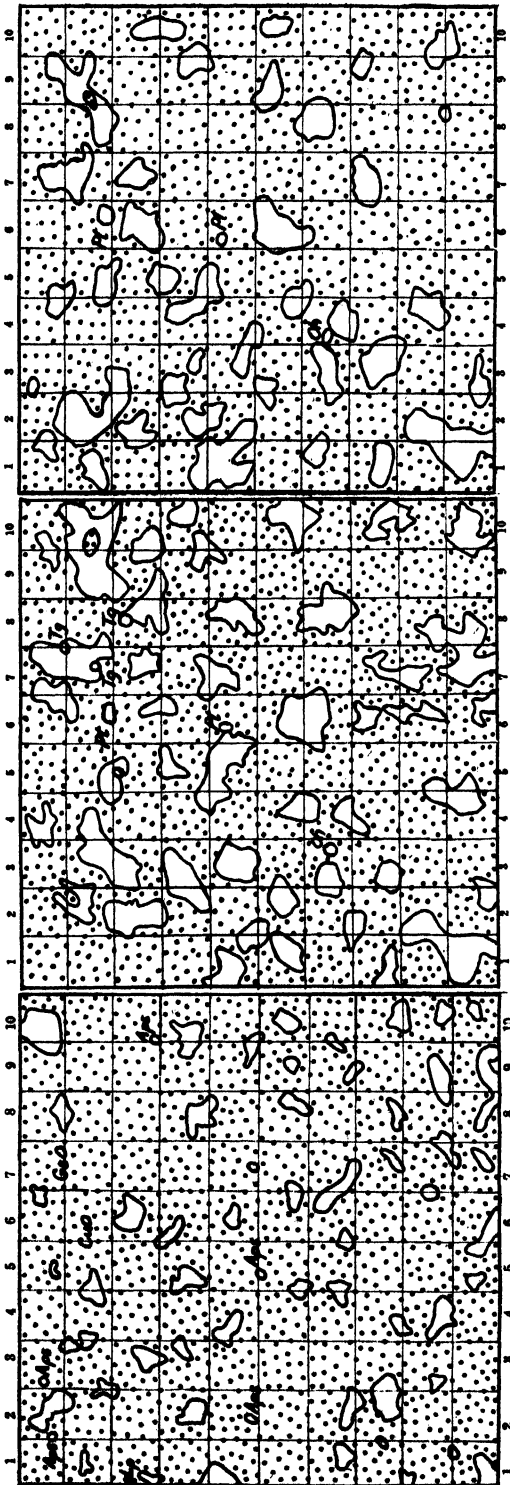


FIG. 36. Quadrat representative of best type of closed short-grass cover on deep, level upland soil. It shows the changes in the native sod pastured lightly until 1932 and ungrazed thereafter. Short grasses are dotted, bare soil is delimited by lines. Basal cover in the fall of 1932 (left) was 90 per cent. It decreased to 79 per cent (center) by the fall of 1934 but, because of the very favorable early summer of 1935, it again increased to 83 per cent (right). Protected areas and pastures moderately grazed before 1932 withstood the drought best. This was largely due to deeper root penetration and more abundant food reserves. Typical forbs, present in 1932 but not found later, are *Ambrosia psilostachya* (Aps), *Cirsium undulatum* (Cu), *Grindelia squarrosa* (Gs), and *Liatris punctata* (Lp). *Opuntia humifusa* (Oh) and *Psoralea tenuiflora* (Pt) both withstood the drought.

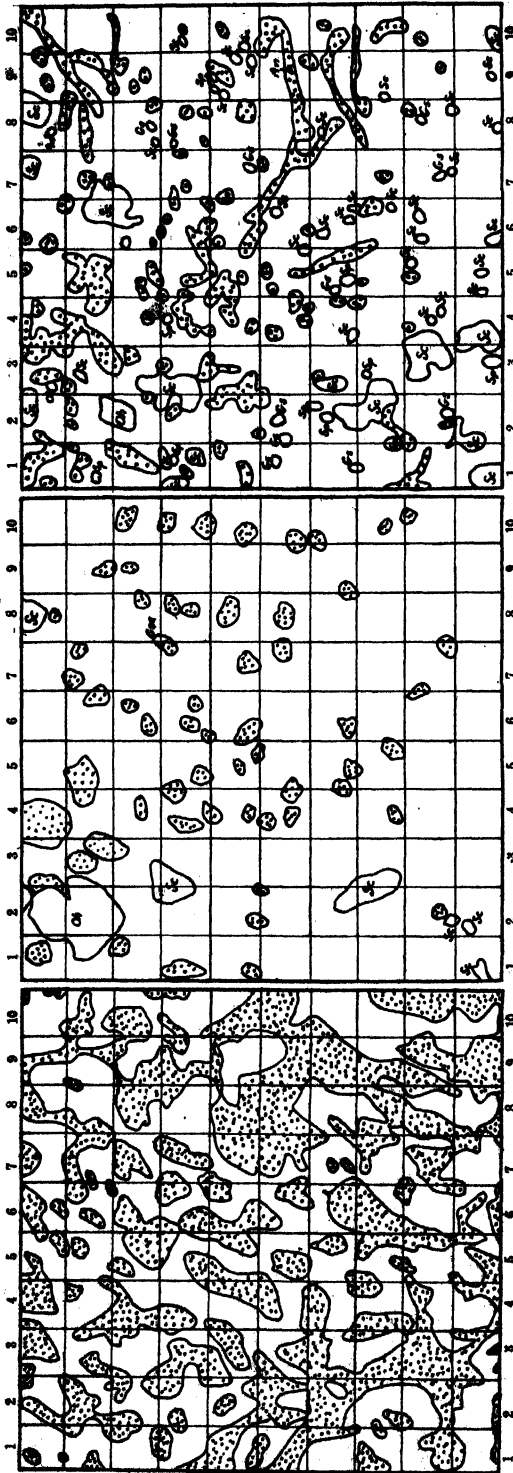


FIG. 37. Quadrat in the open-mat type of *Bulbilis-Bouteloua* short-grass cover showing changes in vegetation resulting from drought. In 1932 (left) 43 per cent of the soil was covered. This was reduced to 8.7 per cent late in 1934 (center), but due to propagation by stolons of *Bulbilis dactyloides* the cover increased to 14 per cent in 1935 (right). *Bouteloua gracilis* made few gains and sustained little loss during 1935. The maximum spread of buffalo grass following the favorable spring and early summer was maintained and was quite in contrast to the heavy losses in the closed-mat, short-grass type, especially under heavy grazing. *Sporobolus cryptandrus* (Sc) increased from 1.3 to 6.2 per cent after most of the sod-forming grasses had died, the old bunches increasing in size and new ones becoming established. *Gutierrezia sarothrae* (Gs) and *Schedonnardus paniculatus* (Sp) were other invaders.

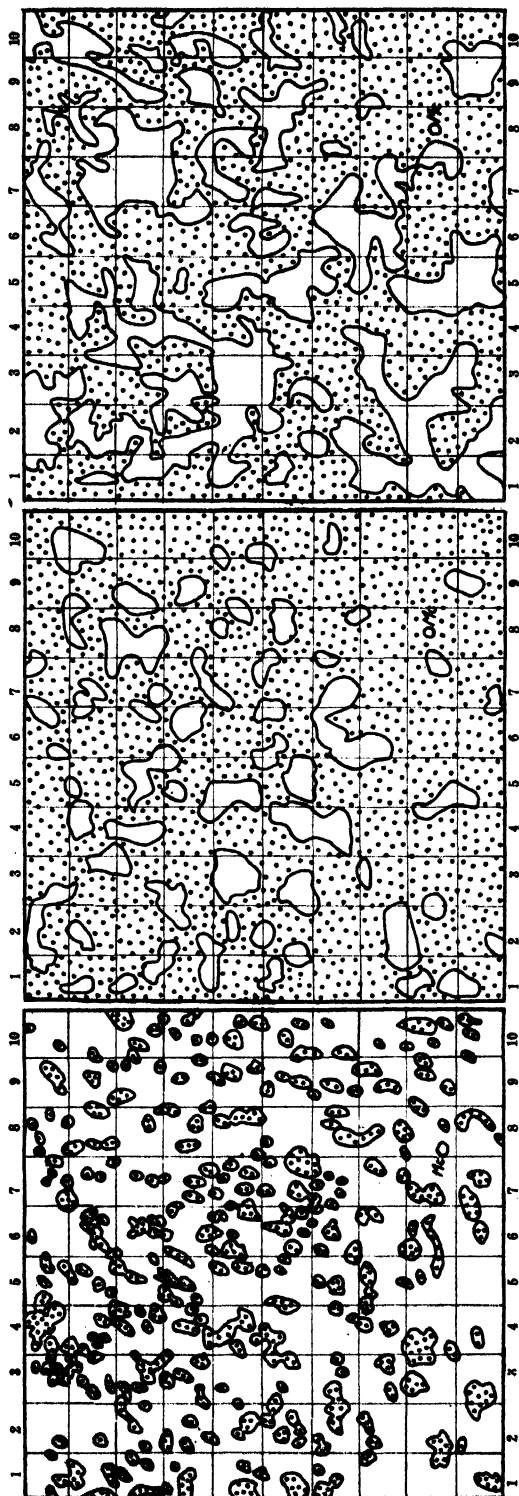


FIG. 38. Quadrat in typical, moderately grazed short-grass type showing living ground cover in the spring of 1935 (left), the maximum live cover during 1935 following good early summer rains (center), and the living cover in the fall. Cover increased from 23.4 to 80 per cent, but during seven weeks of drought decreased again to 63.2 per cent. Increase was due to growth of stolons of buffalo grass. Where the roots from the nodes were sufficiently elongated the grass survived the drought. Where only poorly rooted they died in late summer. Few roots from stolons entered the soil unless the surface was moist. From May 11 to June 28, 14 rains occurred.

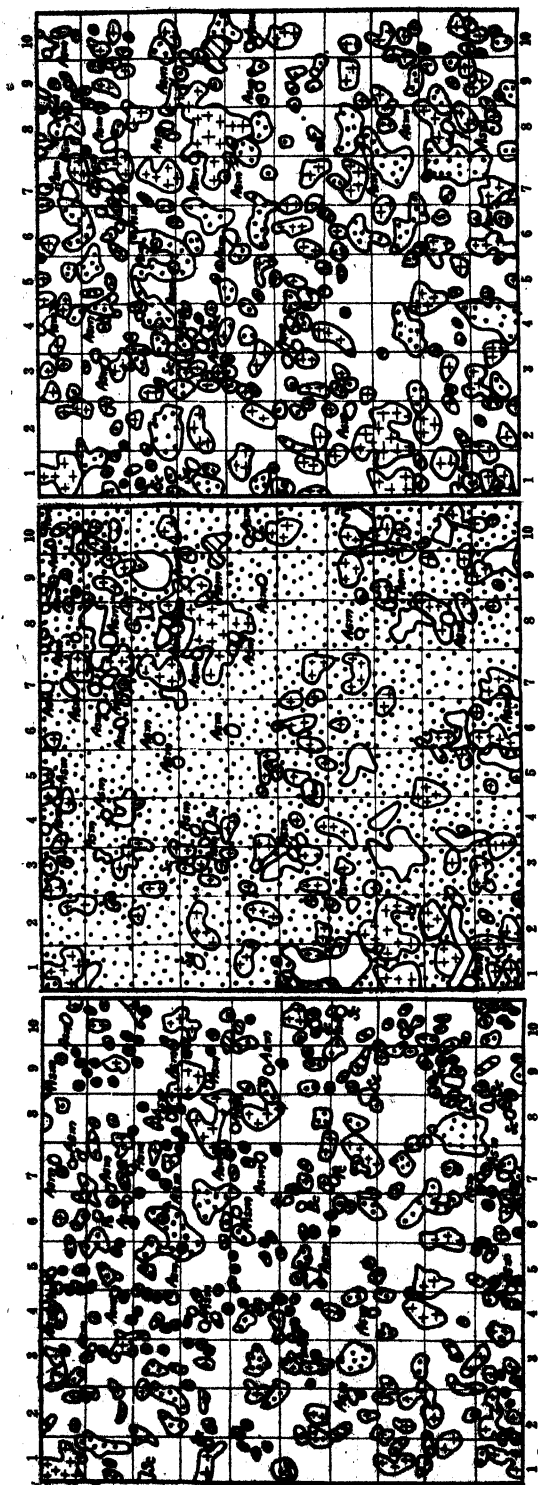


FIG. 39. Relative amounts of living buffalo grass (dots), blue grama grass (crosses), and other grasses in the spring following the great drought of 1934 (left), in the early summer after excellent conditions for growth (center), and after the severe summer drought (right). The 4 per cent increase in blue grama grass is in sharp contrast to the 60 per cent increase of buffalo grass. Stolons grew nearly $\frac{3}{4}$ inch per day and rooted promptly. But drought resulted in such great losses of the new growth that the seasonal increase in basal cover was only from 14.6 to 17.3 per cent. Most of the old plants remained alive. *Agropyron smithii* (Asm), *Bouteloua curtipendula* (Bc), *Sporobolus cryptandrus* (Sc), *S. asper* (Sa), *Panicum capillare* (Pc), and *Aristida purpurea* (Ap) are other grasses that occurred in small amounts.

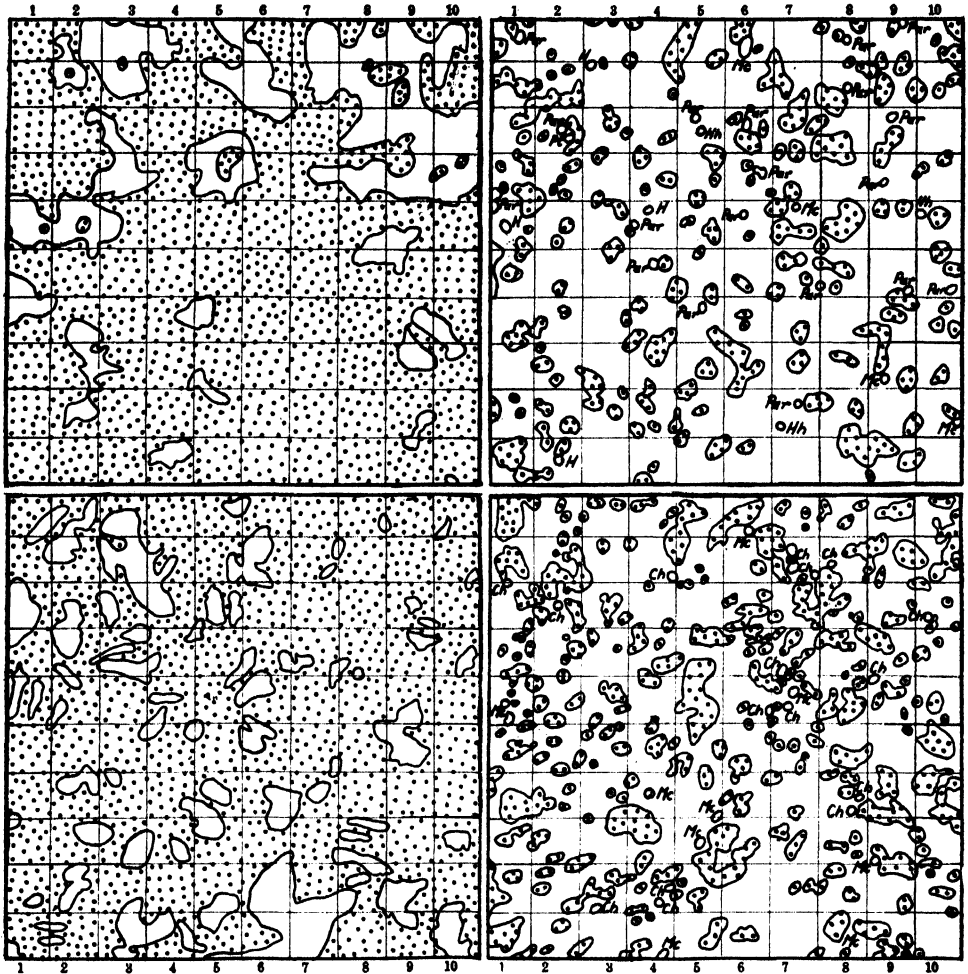


FIG. 40. Quadrat in typical closed-mat, short-grass type (dotted) showing seasonal changes in ground cover. Upper left shows total ground cover (77.5%) during 1934. The living basal cover was reduced to 16.6 per cent (upper right) in the spring of 1935. During the summer it increased to 80.1 per cent (lower left), but decreased to only 25.5 per cent (lower right) after the severe summer drought. *Plantago aristata* (Par), *Hordeum pusillum* (H), *Hedeoma hispida* (Hh), and *Malvastrum coccineum* (Mc) constitute the forbs. *Carex heliophila* (Ch) occurred commonly after the spring rains of 1935.

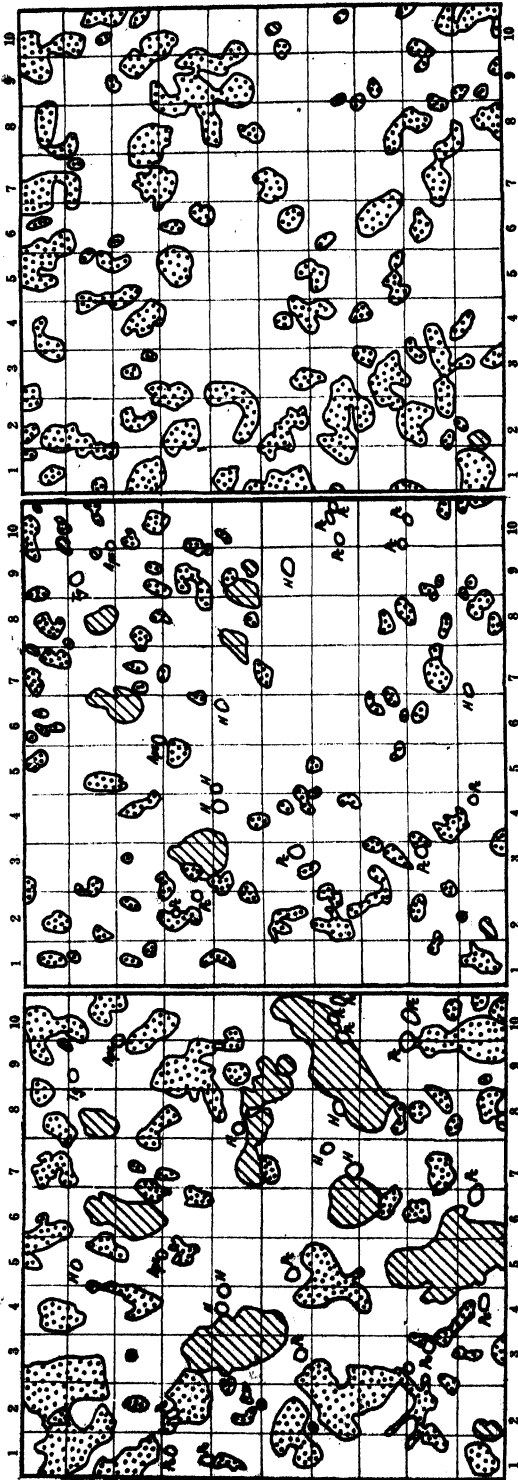


FIG. 41. Quadrat showing the death of wire grass (*Aristida purpurea*) in typical short-grass type as a result of drought. The first charting, June 19, 1935 (left), shows the total cover of vegetation including the dead bunches of wire grass and areas of short grass. The center chart, made on the same day, shows the living basal cover only. The last (right) shows the living basal cover on October 10. *Aristida* (left hatch) was reduced from 8.8 to 2.3 per cent before the 1935 drought, and practically all plants were killed by fall. Short grasses (dotted) were reduced from 21.3 per cent to 10.6, and then by stolon growth of *Bubilis* increased to 21.4 per cent (or more) which gain it held despite the drought of 1935. *Ambrosia pilostachya* (Aps), *Hordeum pusillum* (H), *Panicum capillare* (Pc), and *Thelesperma gracile* (Tg) all died as a result of the extremely dry July and August of 1935.

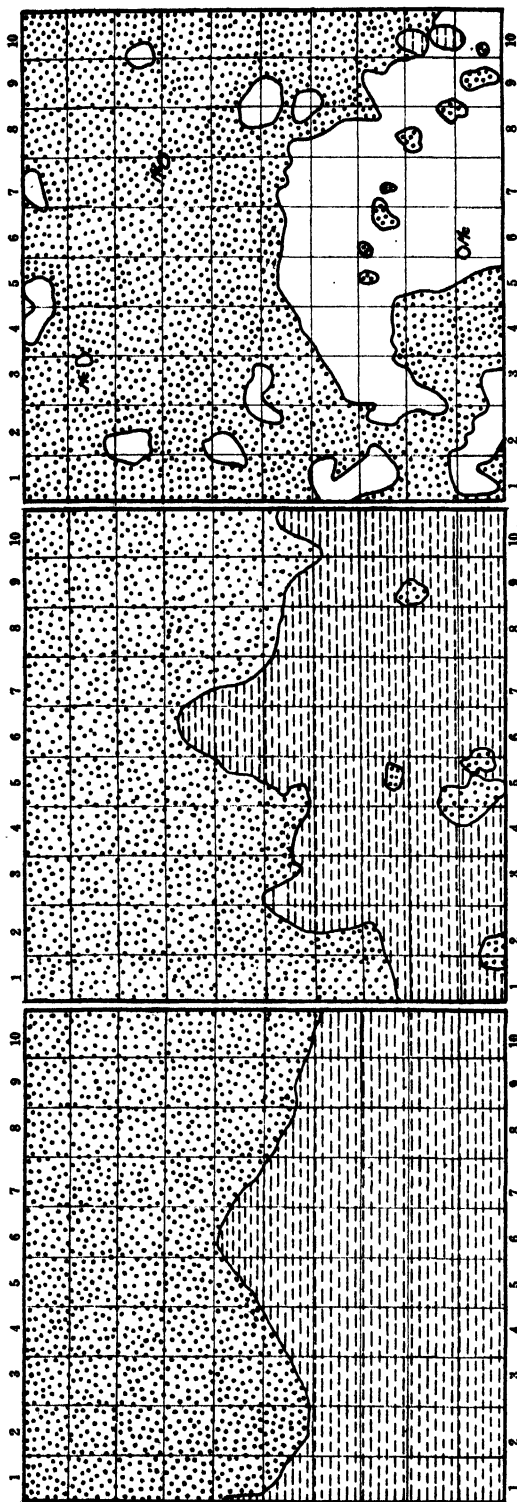


FIG. 42. Quadrats showing invasion of short grasses (dotted—*Bulbilis-Bouteloua* type) into area occupied by slender grama grass (*Bouteloua curtipendula*—broken horizontal hatch) during three consecutive growing seasons under conditions of moderate grazing. In 1933 (left), 46 per cent of the area was occupied by the tall-grass type and 54 per cent by the short grasses. By October 20, 1934 (center), the area of the tall grass had decreased to 41 per cent and the short grasses increased to 59. Buffalo grass was invading the bare area left vacant by the death of the tall grass. At the end of 3 years of drought (right), the tall grass was represented by a .5 per cent remnant. The short grasses, although also suffering some losses, now covered 74 per cent of the ground. This quadrat was located on rather low, slightly sloping land.

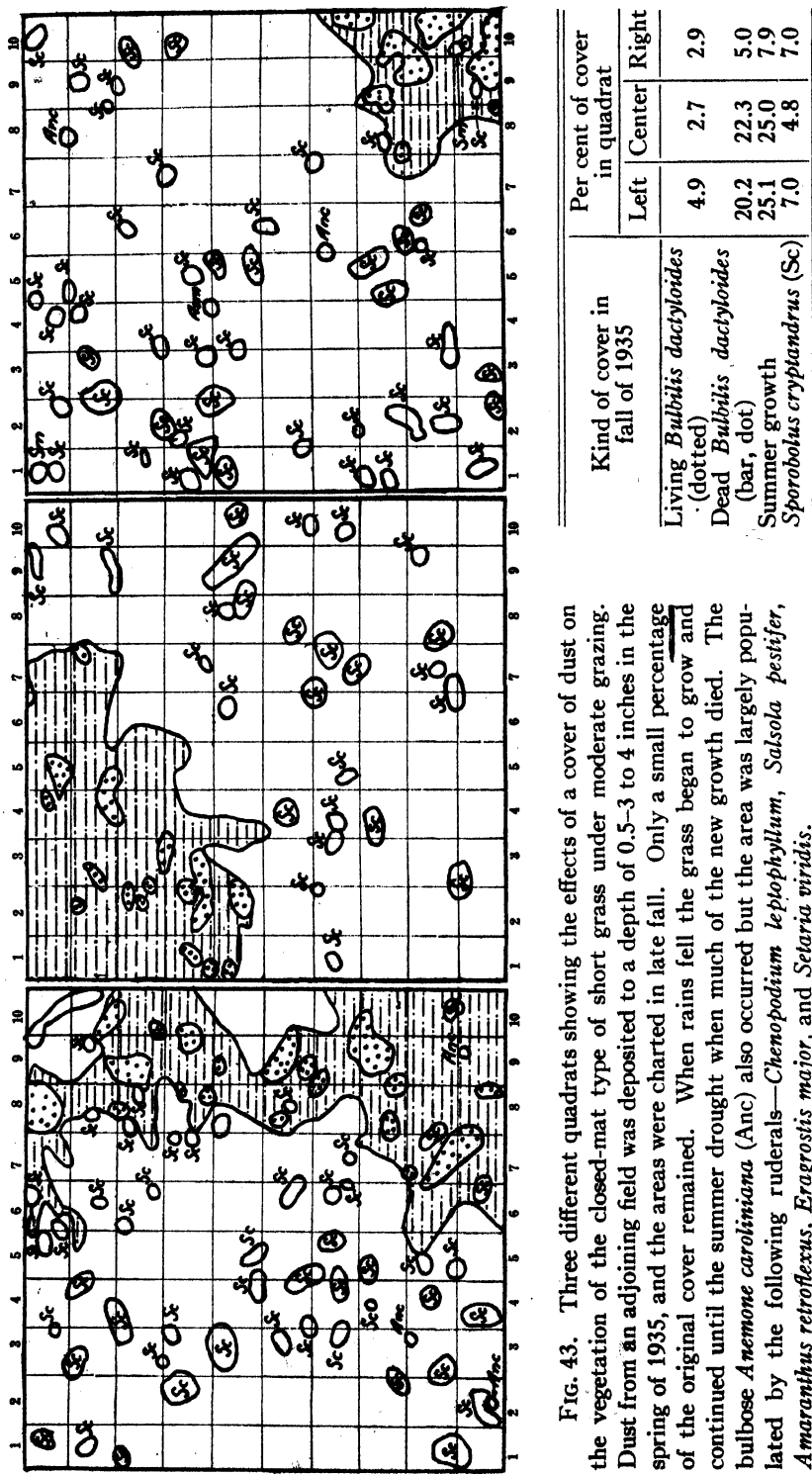


FIG. 43. Three different quadrats showing the effects of a cover of dust on the vegetation of the closed-mat type of short grass under moderate grazing. Dust from an adjoining field was deposited to a depth of 0.5-3 to 4 inches in the spring of 1935, and the areas were charted in late fall. Only a small percentage of the original cover remained. When rains fell the grass began to grow and continued until the summer drought when much of the new growth died. The bulbous *Anemone caroliniana* (Anc) also occurred but the area was largely populated by the following ruderals—*Chenopodium leptophyllum*, *Salsola pestifer*, *Amaranthus retroflexus*, *Eragrostis major*, and *Scleria viridis*.

Little-bluestem type

Little bluestem suffered great losses, even when protected from grazing, especially during the drought of the second and third year when the reserve water in the pockets and crevices of the rocks was exhausted. It was replaced to some extent by big bluestem, slender grama, and species of *Sporobolus*, especially where these grasses were present in the mixture, but much of the soil surface was left bare. Little bluestem was handicapped by a root system which extended only 3 to 3.5 feet deep, those of big bluestem and slender grama penetrated deeper. In the ecotone between little bluestem and the short grasses, where the taller grass gradually spread outward during good years, little bluestem practically all died and much of the area was taken by buffalo grass (fig. 44). Under close grazing, good stands of mixed blue-



FIG. 44. Ecotone between short grasses and little bluestem on the level uplands. Practically all of the bluestem died as a result of drought.

stems on north-facing slopes decreased 66 per cent or more during 1935 alone. Almost total losses of the grass occurred on south-facing slopes.

Data from a group of 52 quadrats in the little-bluestem type are summarized in table II. All quadrats in this and following tables designated as ungrazed were lightly pastured until the spring of 1932, after which stock was excluded. The light grazing prevented the development of a maximum plant cover, which probably resulted beneficially to the plants in reducing total water transpired and in withstanding the following drought. The quadrats in the first group of 8 had a basal cover ranging from 2.5 to 70.3 per cent, which explains the relatively low average for the group. The percentage of loss was 72.

TABLE II. *Changes in percentage of basal cover in little-bluestem type during the drought*

Habitat	Number of quadrats	Treatment	Ave. per cent basal cover			Per cent change basal cover		Per cent	
			1932	1934	1935	Gain	Loss	Gain	Loss
Closed type	8	Ungrazed	35.2	30.9	9.9	—	25.3	—	72.0
Open type	4	Ungrazed	25.3	23.2	12.2	—	13.1	—	51.8
Ecotone between tall and short grass	13	Ungrazed	23.0	5.3	2.7	—	20.3	—	88.2
Ecotone between tall and short grass	13	Moderately grazed	8.7	2.1	0.2	—	8.5	—	97.7
			Spring 1935		Fall 1935				
Closed type	3	Ungrazed	22.9	25.7	2.8	—	12.2	—	
Closed type	7	Moderately grazed	7.64	7.61	—	0.03	—	0.39	
Ecotone between tall and short grass	4	Moderately grazed	4.3	0.3	—	4.0	—	93.0	

The vegetation in the open type withstood drought better than that on the deeper soil during 1934, because of available moisture in the clay pockets in the underlying limestone. The great loss occurred in 1935. Total loss was 51.8 per cent.

Little bluestem covered 2 to 65 per cent of the 13 quadrats in the ungrazed ecotone. Here the greater losses occurred between 1932 and 1934, since the soil was deep and there were no clay pockets with available moisture, at least within reach of the roots. The losses averaged 88.2 per cent. In an adjoining grazed area, where the basal cover varied from 0.5 to 25.3 per cent, the loss was 97.7 per cent. Grazing reduced the size and vigor of the little bluestem and permitted invasion of the short grasses.

Quadrats established in 1935, in little bluestem that had not been grazed for 20 years, revealed a basal cover of only 22.9 per cent. The good development during the wet years resulted in unusual transpirational losses and a thinning of the stand during 1934. A gain of 12.2 per cent was recorded during 1935. Seven moderately grazed quadrats revealed a much lower basal cover in both spring and fall of 1935, with practically no change. Farther up the hill in the ecotone, the little bluestem constituted only 4.3 per cent of the basal cover and short grasses the remainder. Competition of the short grasses for water resulted in a loss of 93.0 per cent of the bluestem. This is in agreement with the losses from the 13 quadrats in a similar area, first charted in 1932.

Table III shows the change in the percentage of *Bouteloua curtipendula*, which is found rather regularly throughout the little-bluestem type. In small areas *Bouteloua* sometimes constitutes the major portion of the plant cover. In an ungrazed, heavy cover it suffered a loss of 59 per cent. Where it constituted only 4.3 per cent of the basal cover in 1934, it made a gain of 37.3 per cent. This corresponds very closely to studies made from 1932-35. Ungrazed quadrats on thin soil underlaid with limestone gave an increase of 54.2 per cent during 1935. The partial basal cover was so low, however, that it allowed considerable experimental error. A group of 6 moderately grazed quadrats gave a loss of 98.2 per cent during 1935. These data show that, in general, slender grama survived the drought when ungrazed (except in heavy stands) but suffered severe losses when grazed. Quadrats charted

TABLE III. *Change in percentage of Bouteloua curtipendula in little-bluestem type during the drought*

Number of quadrats	Treatment	Ave. per cent of basal cover		Per cent change in basal cover		Per cent	
		1934	1935	Gain	Loss	Gain	Loss
4	Ungrazed heavy cover	72.3	29.6	—	42.7	—	59.0
8	Ungrazed light cover	4.3	5.9	1.6	—	37.3	—
4	Ungrazed, thin soil	2.4	1.1	—	1.3	—	54.2
6	Moderately grazed	11.5	0.2	—	11.3	—	98.2
		Spring 1935	Fall 1935				
3	Ungrazed	1.7	4.1	2.4	—	141.1	—
7	Moderately grazed	8.0	8.3	0.3	—	3.7	—

in the spring and fall of 1935, showed gains of 141 per cent when ungrazed and even 3.7 per cent where moderately grazed on a north-facing slope.

Andropogon furcatus is scattered thinly throughout the little-bluestem type. Five quadrats charted in the fall of 1932 and again in the fall of 1935 showed no change, the basal cover afforded by the big bluestem being 7.8 per cent at both times. The area was ungrazed. In 1934, however, the cover had decreased to 2.4 per cent. These data are in agreement with general observations that big bluestem decreased from 1932-34, but increased at the expense of little bluestem during the summer of 1935.

Short-grass type

The best type of closed short-grass cover, protected from grazing during the drought, showed relatively small losses (10-20%) although certain native

forbs entirely disappeared. But in the open-mat type, on less favorable soil, often four-fifths of the cover was lost during 1934 but some of it was regained and maintained during 1935 (fig. 45). Where the short-grass cover had been greatly depleted in 1934, numerous small areas of living plants occurred everywhere. From these sprang stolons of buffalo grass which rapidly and rather completely reclaimed the area in May and June of 1935. Losses of the new growth, following the ensuing drought, varied from 20 to 95 per cent, depending upon type of soil and its available supply of water.



FIG. 45. Detail of remnants of buffalo grass in the open-mat type following the drought. Note the dead plants and the few survivors.

Growth of stolons began in May, 1935, almost immediately following the rains (fig. 46). When they were 6 to 8 inches long, an average daily elongation of .6 inch was observed over a 7-day period very favorable to growth. With the inception of summer drought this decreased to .18 inch, and then to .03 inch on July 13. By July 20 they began to die back from their tips. Bisections made at various places in the short-grass habitat showed that the roots were both more numerous (5.3 against 2.6) and longer (11.7 against 5.5 inches) at the nodes that had not died than on dead nodes of stolons. The average total root length per live node was 62 inches, that of dead ones 14.3 inches. Counts of large numbers of stolons in both overgrazed and undergrazed areas showed that the latter had 20 per cent more nodes and that 30 per cent more of these were alive.

Bouteloua gracilis made but small gains in the short-grass areas despite the 7-week period for growth in 1935, nor were its losses great during the

following drought. Seasonal variations in basal cover were, however, most extreme in the short-grass type. For example, reduction from 80 to 15 per cent during 1934, increase to 80 per cent by the next midsummer, and a decrease to 25 per cent by fall were recorded in ungrazed prairie.

Data from 49 quadrats in the short-grass type are recorded in table IV. Three ungrazed quadrats in the closed type had a basal cover of 88.3 per cent in 1932. This was slightly reduced in 1934, and the total loss was only 8.6 per cent by the fall of 1935. Conversely, 3 quadrats in the open type where the basal cover was 36.7 per cent suffered a loss of 77.5 per cent. The great loss occurred between 1932-34. During 1935, the cover increased from 4.9 to 8.3 per cent.

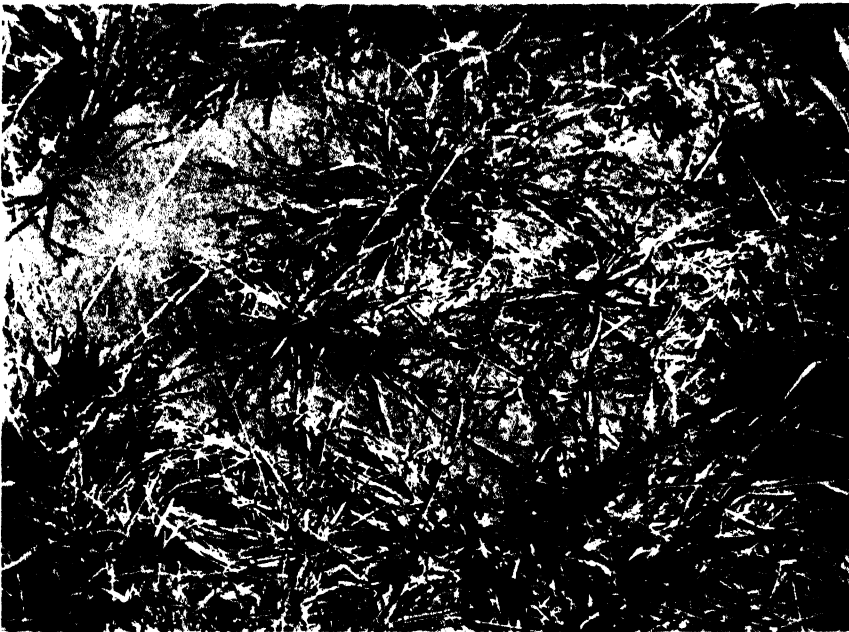


FIG. 46. *Bulbilis dactyloides* at Hays, Kansas, in June, 1935, reclaiming by spread of stolons areas bared during the drought.

Quadrats in ungrazed short grass, with a basal cover of 23.2 per cent, showed gains of 29.3 per cent. Three moderately grazed quadrats, with 15.1 per cent basal cover in spring, increased in cover to 80 per cent by summer. The cover then decreased to 27.2 per cent by fall, but the seasonal gain was 80.1 per cent. In 13 other moderately grazed quadrats the gains were even greater. The basal cover increased 13.9 per cent which was a percentage gain of 111.2. Thus the moderately grazed quadrats, where the original basal cover was low, made the greater recovery.

In the 24 other quadrats (table IV), the percentage of the unit areas occupied by short grasses only was determined. In seven ungrazed quadrats, located where little bluestem and other grasses were not abundant, short grasses

TABLE IV. *Change in percentage of basal cover in the short-grass type during the drought*

Habitat	Number of quadrats	Treatment	Average per cent basal cover			Per cent change basal cover		Per cent	
			1932	1934	1935	Gain	Loss	Gain	Loss
Closed type short grass	3	Ungrazed	88.3	83.3	80.7	—	7.6	—	8.6
Open type short grass	3	Ungrazed	36.7	4.9	8.3	—	28.4	—	77.5
			Spring 1935	Summer 1935	Fall 1935				
Short grass	4	Ungrazed	23.2	—	30.0	6.8	—	29.3	—
Short grass	2	Moderately grazed	15.1	80.0	27.2	12.1	—	80.1	—
Short grass	13	Moderately grazed	12.5	—	26.4	13.9	—	111.2	—
Per cent of square meter occupied by short grasses									
			1932	1934	1935				
Ecotone between tall and short grass	7	Ungrazed	91.7	97.6	98.9	7.2	—	7.8	—
Ecotone between tall and short grass	3	Ungrazed	33.3	48.4	53.0	19.7	—	59.2	—
Ecotone between tall and short grass	14	Moderately grazed	65.9	84.7	94.7	28.8	—	43.7	—

occupied 91.7 per cent of the quadrat. In the fall of 1935, this increased to 98.9 per cent. In three other ungrazed quadrats, where the short grasses covered only one-third of the soil, they increased, as the little bluestem died, until they occupied 53 per cent of the areas. In 14 moderately grazed quadrats short grasses covered 65.9 per cent of the soil in 1932 and 94.7 per cent in 1935. The gain was 43.7 per cent. Since half of these quadrats had an initial short-grass cover of 90 per cent in 1932, their possible percentage of gain was small. Hence, the average was materially lowered. Many of the quadrats showed a gain of 50 per cent or more. These data reveal the distinct trend toward an increase of the short grasses in the ecotone as they were partially liberated from competition by death of little bluestem, wire grass, and other taller grasses.

Aristida purpurea became well established in the short-grass habitat during the favorable years preceding the drought. Although furnishing but a small percentage of the basal cover, it was rather uniformly scattered through-

out. In 11 quadrats charted in the fall of 1932, its average basal cover was 1.08 per cent. It was almost the same (1.05 per cent) in 1934, but decreased to 0.49 per cent by the fall of 1935. Thus the average percentage of loss was 54.6. Six quadrats, charted in the spring of 1935, contained an average basal cover of *Aristida* of 5.05 per cent, of which only 1.75 per cent was alive. By the fall of 1935 the living plants had a basal cover of 2.2 per cent. Hence, the average percentage loss from drought was 56.5. Since the first group of quadrats, charted in 1932 and again in 1934, revealed slight losses until again charted in 1935, it is reasonable to assume that most of the loss of wire grass occurred during the extremely dry winter of 1934-35, and that slight gains were made during the early summer of 1935.

Quadrats in areas covered with dust showed that burial by 0.5 to 1.5 inches of dust often killed the short grasses, but furnished ideal conditions for invasion by weeds.

Big-bluestem type

The effects of drought had not become apparent on the lowlands characterized by the big-bluestem type by the fall of 1933. At this time determinations of the percentage of ground cover and the composition of the vegetation were made in three different prairies, all within 5 miles of Hays. These prairies had not been pastured for many years, except perhaps lightly in winter, but mowed for hay in late summer or early fall. The deep alluvial soil is rich and dark in color to a depth of 3 to 6 feet.

Andropogon furcatus constituted about 75 per cent of the vegetation. *Bouteloua curtipendula*, scattered rather uniformly throughout, *Agropyron smithii*, confined largely to the bases of the slopes, and *Sporobolus asper hookeri* in complete possession of a few, small, local areas, added 15 per cent to the grass population. The remaining 10 per cent consisted of 6 minor species of grasses.

The percentage of ground cover, as determined from a number of quadrats in each prairie, varied from 7.7 to 13.7 with an average of 10.8 per cent in 1933. Similar determinations in the same series of quadrats in the fall of 1935 gave 8.3 to 14.7 per cent with an average of 11.7. These results, checked by other detailed study, indicate that no loss in basal cover had been sustained.

The number of square decimeters in which each of the constituent species occurred was also determined in 1933 and again in 1935. *Andropogon furcatus* and *Elymus virginicus* showed a definite decrease, the first from 92 to 64 per cent of the square decimeter areas; the second from 8 to 1 per cent. These are in accord with general field estimates which indicated that the big-bluestem constituent of the prairies had decreased from 75 per cent in 1933 to 50 per cent in 1935. Conversely, *Bouteloua curtipendula* increased its percentage of areas from 19 to 39, *Sporobolus asper hookeri* from 26 to 39, and *Agropyron smithii* from 0 to 13. Certain other grasses gained slightly. The

forb population remained practically unchanged except that *Aster multiflorus* made very definite gains along the borders and in the driest areas. In these lowland areas soil moisture was not generally depleted until July, 1935.

THE MIXED PRAIRIE AT PHILLIPSBURG

A mixed prairie of about 50 acres lies 12.5 miles south of Phillipsburg, Kansas. It includes much nearly level land and also gentle slopes facing in all directions. In 1933 the bulk of the vegetation consisted of a pure, tall-grass type of about 80 per cent big bluestem and slender grama grass. The big bluestem mostly formed a continuous open sod in which little bluestem was rather poorly represented. About 10 per cent of the area consisted of nearly pure short-grass alternates, mostly blue grama with a small percentage of buffalo grass intermixed or in pure stands. Another 5 to 8 per cent consisted of mixed tall and short grasses. The short grass, whether pure or as an understory, occurred where the topography caused run-off; the bluestems clothed the remainder of the area where run-off was slight.

Aristida purpurea occurred sparingly but scattered plants of *Elymus canadensis*, *Eragrostis pectinacea*, and *Panicum scribnerianum* were common. No wheat grass was found. Forbs were common but none occurred in extensive societies. The most important were *Psoralea tenuiflora*, *Kuhnia glutinosa*, *Solidago mollis*, and *S. glaberrima*, although *Opuntia humifusa* and *Malvastrum coccineum* were also common.

Even casual examination in June of 1935 showed that great destruction had been wrought by drought and wind-blown dust. Over the long, north slope especially, new soil, well consolidated by the abundant late spring rains which followed the most severe period of dust storms, lay 0.5 to over 2 inches deep. There were great losses in the buried alternates of blue grama grass and buffalo grass. The deeper the burial, the thinner were the stands of big bluestem. Over extensive areas where the new soil was 2 to 2.5 inches deep and covered with weeds, big bluestem was entirely absent. Elsewhere it was represented by only a few scattered blades. The new growth of some deeply buried clumps had attained a height of 4 to 6 inches and then died. Undoubtedly much destruction had been wrought by drought before the burial by accumulated dust.

The lower joints of many of the cacti were completely buried. Only a few of even the taller prairie forbs persisted. Soil was heaped about the bases of those that grew. The area had been converted into a great waste now well populated with weeds which varied in height from 8 to 18 inches. Chief among these in order of importance were *Chenopodium album*, *Salsola pestifer*, *Setaria* spp., *Lepidium virginicum*, *Helianthus annuus*, *Amaranthus retroflexus*, *Solanum rostratum*, and *Xanthium commune*.

On the wind-swept slopes and level lands dust deposit was variable but less pronounced. A layer 0.5 to 1 inch thick was usual. Places recurred

where the short grasses were dying, but the new growth of buffalo grass was good where not more than 0.25 inch of soil was deposited. The ground cover was far more open than usual. While some of the dead remains were still plain, the general evidence of death of the vegetation was the extent of bare ground. Little bluestem had been killed everywhere; not a single living plant was found. Careful estimates placed the loss of big bluestem at 35 per cent. Many clumps of half-dead *Sporobolus cryptandrus* were found, while *Elymus* had greatly decreased. Death did not entirely denude large areas but resulted in greatly thinning the stand. In some places big bluestem had lost half of its holdings. Hence an irregular but continuous pattern of bare ground was the rule. Sometimes destruction of the grass was fairly complete. Over great stretches, however, some good big bluestem still survived.

The degree of destruction was clearly indicated in most places by the abundance of weeds. Their height varied somewhat directly with the depth of deposited soil. The weeds of north slopes also ranged throughout, varying from thinly scattered growths to dense stands.

The upper story of *Psoralea tenuiflora* was fairly well intact, *Gaura coccinea* was common, *Malvastrum coccineum* formed a common ground pattern, and in the ravines the dense growth of *Solidago mollis* reminded one of the usual buckbrush eastward. *Ambrosia artemisiaefolia* formed thick growths in a few of the ravines and *Aster multiflorus* was well developed locally. The understory of *Panicum scribnerianum*, *Antennaria campestris*, species of *Viola*, and even most of *Astragalus crassicaulus* had disappeared.

A fine level tract of mixed prairie lies near Phillipsburg. It has been studied at intervals for the past 15 years (Weaver, '24). The loess soil is a mellow, dark-brown, fine sandy loam of the Colby series.

The vegetation was typical mixed prairie, the tall grasses alternating with or forming a layer above the shorter ones. *Andropogon scoparius*, *A. furcatus*, and *Sorghastrum nutans* formed more or less continuous sodded areas varying from 6 inches to 7 feet in diameter where short grasses were often almost entirely excluded. *Bouteloua curtipendula* and *Elymus canadensis* were other important grasses. Alternating with these were similar or, in drier places, even larger areas of *Bulbilis dactyloides* and *Bouteloua gracilis*, intervening areas, often to the extent of one-fourth of the surface being nearly devoid of vegetation. More usually, however, the short and tall grasses were intimately mixed, the latter often showing strong tendencies toward the bunch habit.

In the fall of 1933 it was observed that great injury to the bluestems had resulted from the summer drought. Nearly all of the bunches or mats of sod were partly killed and in many places the entire tops were dead and brown, separating easily from their bases as if decayed. Little bluestem seemed less affected than did big bluestem. *Panicum virgatum* was green even in the center of patches of big bluestem, probably because of its very deep root system. *Bouteloua gracilis* and *B. hirsuta* were both rapidly producing flower

stalks after the cessation of drought. *Aristida purpurea* had seeded at about the normal height. *B. curtipendula* had been injured considerably by the drought. The brown patches of the tall grasses showed conspicuously against the green pattern of the shorter ones and indicated clearly what would happen should drought years continue.

Further study in the midsummer of 1935 showed that the tall grasses had practically all succumbed to the continued drought. This prairie had escaped any burial by dust. A living little bluestem was not found although the dead bases were plentiful. Big bluestem had likewise disappeared except in the depression of an old road. *Sorghastrum nutans* had died, *Elymus canadensis* was found only in the road, and only mere relicts of *Bouteloua curtipendula* were seen. Even many plants of *Opuntia humifusa* had died. Thus the once well developed upper story of tall grasses had disappeared except for a very scattered growth of *Sporobolus cryptandrus* and *Aristida purpurea*.

The short grass vegetation was in a thriving condition and blossoming profusely. This resulted from the abundant rainfall which was no longer shared by the tall-grass layer, nor were these short grasses handicapped by shading. The long stolons of *Bulbilis* were spreading rapidly over the dead clumps of tall grasses. Many bared areas were already half sodded by the abundant tuft-producing stolons. Blue grama grass was also increasing its territory by filling in the bunches with new stems, by spreading slightly by tillers, and also by the production of seedlings. The foliage cover of these grasses had increased greatly by the spreading of the tops over portions of the adjacent bare areas. The average foliage cover was not more than about 60 per cent, and only 40 per cent where the tall grasses were best developed. But in the local patches of short grasses it was 80 to 100 per cent. The basal cover had been reduced in proportion to the death of the tall grasses except for such gains as were made by the spreading of the short grasses.

Weeds were few; most of the bared spaces still remained free of invaders. *Festuca octoflora* and *Hordeum pusillum* occurred sparingly in bunches. *Lepidium virginicum* was scattered over the bared places as were also some *Salsola pestifer* and *Setaria viridis*. Seedlings of the cacti were common. Forbs were not greatly in evidence; none had become weedy nor made noticeable gains.

By September drought had killed most of the new growth of buffalo grass. Annual weeds, as on the preceding prairie, were very abundant.

GROUPS OF MIXED PRAIRIES

Thirty-one areas of grassland extending across west-central Kansas, were studied, some at two or more periods, between October, 1934, and the fall of 1935, for the purpose of determining losses due to drought. Percentage of ground cover was compared with the normal cover as based upon previous examination and comparisons with similar prairies at Hays. Because of

local distribution of rains during the drought, the results may be conveniently presented by placing the prairies into three groups. In each group, ungrazed, moderately grazed, and heavily grazed prairies were studied (fig. 47).

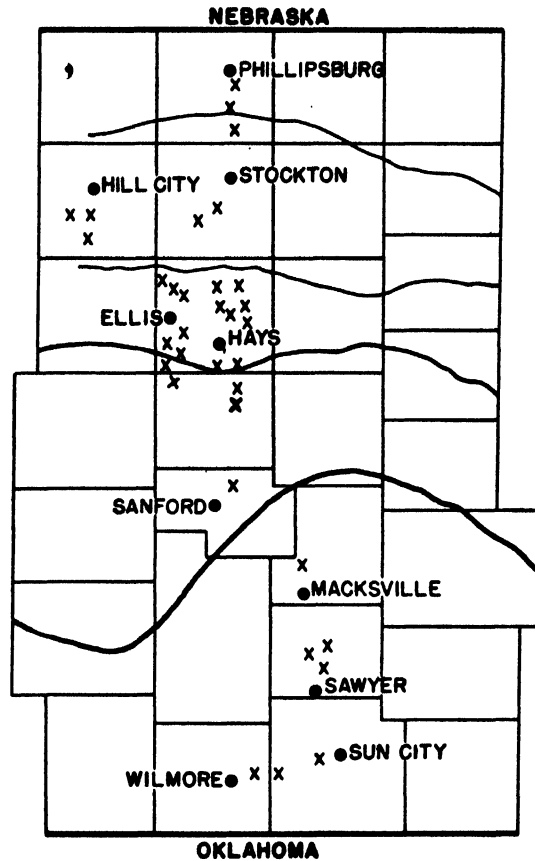


FIG. 47. Location of grassland areas studied in the mixed prairie of west-central Kansas. Phillipsburg is 65 miles due west of Montrose, Kansas (fig. 2), which was the most westerly station studied in the tall-grass prairie.

Prairies south of Hays

Twelve prairies 8 to 116 miles south and southeast of the base station were studied. The soil varied from a heavy clay loam to light sandy loam. *Bulbilis dactyloides* and *Bouteloua gracilis* were the chief grasses on the heavier soil types, the former appearing to survive better than the blue grama where grazing was heaviest. Where rains fell on a considerably reduced ground cover, stolons of buffalo grass spread rapidly. On lighter soil types, buffalo grass was rare, and rather large, distinct bunches of blue grama grass occurred. Soil around the bunches had been gradually removed by the wind, leaving the plants on small mounds. Thus exposed the soil rapidly dried and large dead clumps were common. On rough land, where grazing

had not been too severe, little and big bluestem were dominant, but on similar heavily grazed areas they had disappeared.

Drought had been less severe than either north or west of Hays. This was clearly shown not only by smaller losses among prairie plants but also by the better growth of winter wheat. It was also indicated by the presence of *Antennaria campestris*, *Festuca octoflora*, and certain other species not found elsewhere. The short grasses began to grow in April, and many of the stolons were alive, a phenomenon not found elsewhere in this Kansas area. A heavy growth of little bluestem had resulted from the wet years preceding 1933. Here, losses were especially great during the drought.

Loss of ground cover varied from 30 per cent on moderately grazed prairies to 74 per cent on some heavily grazed. An average loss of 36 per cent from six moderately grazed prairies was determined. These prairies had a development of plant cover which did not use water in excess but furnished adequate protection to the soil against desiccation by wind.

Losses in five heavily grazed prairies ranged from 47 to 87 per cent with an average of 74. Losses in some cases were greatly accelerated by severe trampling as the hungry cattle wandered about. In these heavily grazed areas there was a considerable increase of the following prairie forbs: *Plantago purshii*, *P. spinulosa*, *Diaperia prolifera*, *Lappula texana*, *Cryptantha crassisejala*, *Artemisia* sp., and *Antennaria campestris*.

Prairies north of Hays

Eight prairies lying 12 to 62 miles north of Hays were examined, mostly at two or three different periods. The soil of the rolling to hilly topography varied in texture from sandy loam to clay loam. Short grasses dominated in grazed areas except on rough land near streams characterized by limestone outcrops, where little bluestem was usually dominant.

Loss of ground cover ranged from 50 per cent on one ungrazed area to 98 per cent on heavily grazed ones. The lower portions of the area, ungrazed for many years, had been rather continuously cut for hay. The greatest losses occurred where the vegetation had grown most luxuriantly on the upland during the wet period before the drought. On the highest portions of the prairie, dead crowns of *Andropogon scoparius*, 3 to 14 inches in diameter, were found. Farther down the slopes and on lowlands relatively slight losses had occurred. Thus the great losses on the higher ground largely account for the high average loss.

Three moderately grazed prairies presented an average loss of 54 per cent. Two were primarily short-grass areas where the ground cover was reduced by drought to 60 and 70 per cent, respectively. The third, dominated by little bluestem, suffered a loss of only 43 per cent.

The heavily grazed prairies, on rough limestone outcrops covered by the little-bluestem type, suffered most severely on the south exposures. Here the

cover of grass was often reduced to less than 1 per cent. The following forbs constituted nearly all of the remainder of the vegetation: *Gutierrezia sarothrae*, *Leucelenc cricoides*, *Comandra pallida*, *Echinacea pallida*, and *Lesquerella ovalifolia*. North-facing slopes were also greatly overgrazed but the ravages of drought were less marked.

Vegetation on sandy land, where heavily grazed, suffered very severely from drought, losses often amounting to 95 or even 100 per cent. Native grasses were commonly replaced by *Gaillardia pulchella*, *Helianthus petiolaris*, *Croton texensis*, *Setaria viridis*, *Psoralea lanceolata*, and *Salsola pestifer*.

The short-grass cover of buffalo grass and blue grama on the heavy-textured upland soils often sustained losses of 95 to 98 per cent under heavy grazing. During the moist early summer of 1935 the stolons of buffalo grass grew rapidly and covered many bared areas. They failed, however, to survive the hot, dry portion of the summer and consequently died back, leaving the same meager cover found in the spring.

Prairies west of Hays

Seven prairies 15 to 56 miles northwest of the base station, and four approximately 20 miles southwest were repeatedly examined. The soils varied in texture from the heavy loams of uplands where short grasses prevail to the sandy loam commonly found near the Smoky Hill River. They also included limestone outcrops where little bluestem was prevalent. This group of prairies sustained the greatest average loss of all—84 per cent, ranging from 70 per cent on an area moderately grazed to 96 per cent on a similar one heavily grazed. In heavily grazed pastures the cattle had not only eaten practically every vestige of green but also in desperation had gnawed into the crowns and roots of the grasses devouring them with the attached soil. The dried dung, unlike that resulting from normal herbage, was heavy, since it incorporated quantities of soil. Such extreme signs of overgrazing and drought were rather general.

The only ungrazed prairie found had developed such an excellent cover during years of good rainfall that the reduction of 14 inches in the annual rainfall decreased soil moisture to a point where the demands of the growing vegetation could not be met. The result was the death of the vegetation over large areas and an average loss of 85 per cent. An adjoining, moderately grazed area used the water more conservatively and maintained a considerably higher living basal cover. This was the usual condition; moderately grazed areas suffered less. In these prairies the average loss was 72 per cent. This high loss resulted from increased intensity of drought west of Hays.

The soil was almost bare on heavily grazed prairies. Over many square meters not a living forb or blade of grass could be found. The average loss in this group was 91 per cent in the spring of 1935 and remained thus until

after the late summer rains. Then considerable growth occurred. By December, buffalo grass had spread widely, thus illustrating the wonderful recuperative powers of the vegetation after three years of drought.

Losses in the little-bluestem type were slightly less. Here some bunches were so favorably rooted in the deep, moist soil of crevices and pockets of the limestone that they lingered on despite the drought.

The sandy soil was clothed with mixed tall and short grasses of which *Andropogon scoparius*, *Sporobolus cryptandrus*, *Bouteloua curtipendula*, and *B. gracilis* were most important. The plants commonly occurred in bunches or mats with much bare soil between. Heavy grazing and drought had resulted in the death of most of these. In many places the dead crowns remained intact (fig. 48).



FIG. 48. Pasture 50 miles west of Hays, Kansas, in fall of 1935. The dead remnants of the bunches of little bluestem are all that remain of the plant cover.

A summary of the losses in the 31 prairies studied, together with the type of treatment, is given in table V.

Where the prairies were located near cultivated fields, a layer of dust 0.5 to 4 inches in depth commonly covered the vegetation. The depth often varied directly with the density of the plant cover, being greatest where it was heavy. In many places where weeds had blown into the fences and formed a barrier to wind-blown dust, great drifts accumulated over the fences and extended outward over the grassland (fig. 49). Where the new deposit was more than an inch in thickness, loss of vegetation was practically complete. Farther out in the prairie, deep drifts of dust accumulated over the

TABLE V. *Loss in plant cover in various types of Kansas prairies under different treatments*

Type of prairie	No.	Direction from Hays	Treatment	Per cent loss	Ave. per cent
Little bluestem	1	110 mi. S.	Ungrazed	60	60
Little bluestem	1	115 mi. S.	Moderately grazed	30	36
Mixed	2	98 mi. S.	" "	35	
Short grass	3	15-100 mi. S.	" "	44	
Short grass	5	8-116 mi. S.	Heavily grazed	74	74
Little bluestem	1	14 mi. N.	Ungrazed	50	50
Little bluestem	1	15 mi. N.	Moderately grazed	43	54
Short grass	2	12-61 mi. N.	" "	65	
Little bluestem	2	16-61 mi. N.	Heavily grazed	90	91
Mixed	1	18 mi. N.	" "	96	
Short grass	1	62 mi. N.	" "	88	
Little bluestem	1	50 mi. N.W.	Ungrazed	85	85
Little bluestem	1	56 mi. N.W.	Moderately grazed	70	72
Short grass	2	18-30 mi. N.W.	" "	75	
Little bluestem	2	22-25 mi. N.W.	Heavily grazed	89	91
Mixed	1	55 mi. N.W.	" "	95	
Short grass	4	15-25 mi. S.W.	" "	39	



FIG. 49. Wind-blown dust caught by snow fence in west-central Kansas. Photo by G. E. Condra, April 1935.

bunches of grass, which resulted in their death. Where the ground was nearly bare and the living portions of the grass remnants were below or just above the surface of the soil, the layer of dust was comparatively thin and losses caused directly by it were usually small.

Dust, even from distant fields, carried with it myriads of seeds of the weeds common to cultivated land. Seeds of Russian thistle, tickle grass, etc.,

scattered far by plants tumbling before the wind, were even more widely distributed during the "black blizzards."

CHANGES IN POPULATIONS OF GRASSES AND FORBS

Certain grasses, found regularly in the prairies of midwestern Kansas during preceding years, were so adversely affected by the drought that during 1934-35 they were found only occasionally. Chief among these were *Eatonia obtusata*, *Koeleria cristata*, *Poa arida*, *Panicum scribnerianum*, *Aristida purpurea*, *Festuca octoflora*, and *Alopecurus geniculatus*.

The following forbs, although not affected to the same extent by the drought, were either partially or completely eliminated from the prairies: *Achillea lanulosa*, *Ambrosia psilostachya*, *Anemone caroliniana*, *Antennaria campestris*, *Astragalus missouriensis*, *Astragalus shortianus*, *Castilleja sessiliflora*, *Cerastium brachypodum*, *Erigeron ramosus*, *Myosurus minimus*, *Oxytropis lambertii*, *Polygala alba*, *Psoralea argophylla*, *Sophora sericea*, *Specularia leptocarpa*, *Specularia perfoliata*, *Spermolepis divaricata*, *Tithymalus missouriensis*, and *Viola rafinesquii*.

The decrease in ground cover occasioned by the death of the grasses and forbs resulted in an increase in the numbers of certain native forbs of greater drought resistance. Those that spread most conspicuously were as follows: *Artemisia* spp., *Aster multiflorus*, *Diaperia prolifera*, *Echinacea pallida*, *Gutierrezia sarothrae*, *Malvastrum coccineum*, *Oxalis stricta*, *Plantago purshii*, *Plantago pusilla*, *Plantago spinulosa*, *Polygala verticillata*, *Quincula lobata*, *Solidago mollis*, and *Verbena bracteosa*.

Seeds of ruderals had been spread widely by the wind over the whole midwest. Ecesis in the bared areas was prompt upon the advent of rain. Consequently most prairies and pastures were literally covered with seedlings of species of *Chenopodium* and *Amaranthus*, *Eragrostis major*, *Panicum capillare*, *Setaria viridis*, *Solanum rostratum*, *Lepidium virginicum*, *Salsola pestifer*, *Bromus tectorum*, and *Hordeum pusillum*.

So abundant were the weeds, that the prairies often appeared more like abandoned fields than grassland. The tallest weeds had rather completely covered the ground, but the summer drought of 1935 had killed most of them before they were fully grown. The most conspicuous species were *Salsola pestifer* and *Solanum rostratum*. *Eragrostis major* and *Panicum capillare* often formed a larger percentage of the ground cover than did the native short grasses. In sandy soil the weed population was fully developed. Large areas were often completely occupied by *Helianthus annuus*, *Chenopodium album*, *C. lanceolatum*, *C. leptophyllum*, *Amaranthus retroflexus*, *Solanum rostratum*, and *Salsola pestifer*.

SUMMARY

Following the most severe drought ever recorded in the prairies of Iowa, Nebraska, and Kansas, studies were made to determine the effects upon the vegetation.

The 30 or more prairies examined in Iowa, Nebraska, and east-central Kansas had each been fully studied before the drought so that changes were readily determined. Prairies on the deep loess soil of southwestern Iowa as well as some northeastward on the glacial soils had not been harmed. Others had suffered a loss of 20 to 50 per cent of certain grasses on the most exposed slopes.

Death by drought increased southwestward, varying from 20 to 50 per cent on thinner soils of exposed ridges to 80 to 95 per cent losses on nearly level areas farther west. Great destruction also occurred even on low ground, sometimes resulting in an entire change in plant populations even in eastern Nebraska.

All of the native grasses suffered some loss, but death was greater among those with relatively shorter roots: *Andropogon scoparius*, *Koeleria cristata*, *Stipa spartea*, and the invading *Poa pratensis*. This often occurred everywhere but especially where they occupied the drier soils. *Sporobolus heterolepis* also sustained losses which, like those of *Sorghastrum nutans*, often amounted to 80 or more per cent. *Andropogon furcatus*, because of its deeper root system, was usually injured least.

Losses among interstitial, low grasses and forbs were often practically complete after the protecting cover of tall grasses dried.

Invasion by the drought-resisting and rapidly spreading *Agropyron smithii* was rapid and locally complete. It occurred widely. *Bulbils dactyloides* and *Festuca octoflora* were other native grasses that increased greatly, especially westward.

Among native forbs that spread most widely, when death of the dominants decreased competition, were *Aster multiflorus*, *Erigeron ramosus*, *Silene antirrhina*, and *Specularia perfoliata*.

Certain ruderals, normally not found in prairies, were widely distributed. The most conspicuous were *Lepidium virginicum*, *Leptilon canadense*, *Bromus secalinus*, and *Tragopogon pratensis*.

Severity of drought in the mixed prairie was studied intensively at Hays, and from the Nebraska to the Oklahoma border in west-central Kansas.

The drought years of 1933 to 1935, when the mean annual precipitation was only 15.4 inches, were preceded by 6 years with an average precipitation 4.9 inches above the normal (22.8 in.). Scores of permanent chart quadrats were marked out, many before the beginning of the drought.

Water content of soil was exhausted to or almost to the depth of root penetration (3.5 to 6 ft.) of the dominant grasses. This occurred at a time when the average day temperatures were 86° to 97° F. and relative humidity was very low. The severe conditions were aggravated by high winds and often by dust storms.

Andropogon scoparius suffered losses of 90 to 100 per cent where it was intermixed with the short grasses. In its typical consociates, losses of 50 to 87 per cent occurred where it was ungrazed and 66 to 96 per cent under

moderate grazing. Moderate grazing preceding the drought, reduced the density of the cover and enabled the vegetation to survive longer on the remaining soil moisture. *Bouteloua curtipendula* and *Andropogon furcatus*, both intermixed with but rooted more deeply than *A. scoparius*, although at first suffering losses, increased with temporary conditions favorable to growth and partially replaced little bluestem.

The closed type of *Bulbilis-Bouteloua* showed relatively small losses when protected from grazing, although certain native forbs entirely disappeared. Losses in open, ungrazed short grass were 70 to 80 per cent. In both types, stolons of *Bulbilis dactyloides* rapidly reclaimed bare areas when moisture was available for growth. Gains of 30 to 111 per cent in basal cover over that of 1932 were recorded in the fall of 1935. There was a marked tendency for this grass to reclaim areas bared by the death of the taller grasses.

At Phillipsburg the mixed prairie was temporarily converted into pure short grass by the death of the bluestems and other tall grasses. Other prairies were buried by dust and converted into waste areas populated by weeds.

Ungrazed prairies of south-central Kansas lost 60 per cent of the basal cover; various types moderately grazed, 36 per cent; and others heavily grazed, 74 per cent. Losses in the same sequence in north-central Kansas were 50, 54, and 91 per cent, respectively.

Conditions were most severe in the west-central part where ungrazed prairies lost 85 per cent, moderately grazed areas 72 per cent, and heavily grazed ones 91 per cent.

Deficient soil moisture, coupled with extremely high temperatures and low humidities, and supplemented by wind and burial by dust, was the cause of the destruction.

Lists of native grasses that entirely or almost entirely disappeared, and native forbs that increased in abundance are given. Weeds sowed widely by the wind and growing in such abundance as to give native grassland the appearance of abandoned fields are also listed.

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MORTALITY OF FISHES DUE TO COLD AT SANIBEL ISLAND, FLORIDA, 1886-1936

MARGARET STOREY

Stanford University

AND

E. W. GUDGER

American Museum of Natural History

There seem to be few accounts in the literature of the killing of fishes by unusually low temperatures. This is especially true for the region under consideration. So far as we can ascertain there are but three brief published records of such mortality on the southern and western coasts of Florida. A. S. Packard, Jr. ('71) gives specific data for Key West (110 miles south of Sanibel) for December 24-25, 1856 and for December 25th, 1868, with a note that on the second date the devastation extended as far north as Tampa (120 miles north of Sanibel). In 1887 Joseph Willcox recorded a cold wave occurring January 12th, 1886 which affected fishes from Cedar Keys (200 miles above) to Punta Rassa (at the mouth of the Caloosahatchee, the river off which Sanibel lies). R. H. Finch ('17), assistant in the U. S. Weather Bureau, has described the destruction of fishes from Key West to Cedar Keys in 1886 and also on February 3rd, 1917. No temperatures are given for the Sanibel region.

UNPUBLISHED DATA FOR FREEZES AT SANIBEL, 1886-1934

Since we can find no discussion of the effects of several freezes upon the fishes in a single locality it seems well to put on record the accounts we have been able to collect, with our conclusions. On Sanibel the word "freeze" connotes not necessarily freezing temperatures but frost or unusually disagreeable cold weather often involving destruction to vegetation as well as death to fishes. The dates and official temperatures are from the records of the U. S. Weather Bureau at Fort Myers (Bennett, '33), the nearest station to Sanibel. Since that city is 20 miles away across San Carlos Bay and up the Caloosahatchee, thus being situated somewhat inland, its temperatures are apt to vary considerably from and often disproportionately to those at Sanibel.

Throughout we have tried to follow local usage in fish nomenclature. At the end of the account we have listed these fish names alphabetically with names common elsewhere and so far as possible scientific names of the fishes mentioned. In most cases laboratory identifications of fishes collected on the spot have been made.

For our first hand accounts of the destruction of fishes and vegetation in the Sanibel region we are indebted to Messrs. Web Shanahan, George Underhill and Sam Woodring. These men, long residents of the island, are known to us as experienced fishermen and reliable observers. Their evidence is definite and conclusive. The data for the freezes of 1928 and 1934 are mainly from the notes and memoranda made at those times by Dr. Louise Merrimon Perry for 17 winters a resident of Sanibel and a keen student of the natural history of that island. All these data will now be presented chronologically.

1886. The only official temperature record we have for that year for southwest Florida is that of Key West, 41° F. on January 12th. Sanibel temperatures would run far below this of course. Unfortunately there are no longer any eyewitnesses to the destruction at Sanibel, but our informants tell us that their elders called "the '86 freeze" the worst that had been known at Sanibel before or since.

1894-1895. During this winter there were two freezes on Sanibel, that of December 29-30, 1894, being the more destructive to fishes. With the possible exception of the 1886 freeze the largest mortality in recent years probably occurred on that date. The cold lasted for a night and a day. Readings as low as 28° F. were made near the salt water. Ice half an inch thick formed in cisterns and rainbarrels. Official minimum for Fort Myers is 24° F. for this date. According to Mr. Underhill it turned warm and rained after the freeze.

Not only were vast quantities of shallow water fishes killed but even many deeper water species. The fishes least injured were the larger mullet, sheep-head, trout, bluefish, redfish, mackerel, and pompano. Of these many were numbed but recovered before they washed ashore. Mortality was highest among the tarpon, gaff-topsail catfish, silver mullet, and permit. Sharks and jewfish were numbed or killed outright. Many brown-spotted eels, probably *Mystriophis intertinctus* (Richardson), from one to six feet long were left dead on the grass flats by the outgoing tide. "The tide went way out and stayed out three days." (See discussion.) Turtles were too paralyzed to swim. A 75 pound green turtle floated onto an oyster reef and was captured. The day after the extreme cold the dead fishes really began to come ashore. The banks of the Caloosahatchee were "white with tarpon," and the shores of Sanibel were lined with all sizes and kinds of fishes from alongshore minnows to huge tarpon. Each succeeding tide brought in more victims ranging them in new lines till they lay, tier after tier, stretching along the beaches as far as eye could reach. Of the smaller fishes the pinfish seemed hardier than most; at least few specimens of this very common little fish came ashore dead, while the less abundant red-spots (young Lane snappers) died by the thousands.

The damage to vegetation was very great. The common buttonwoods

and red and white mangroves, especially the younger growth, were mostly killed outright, the rest destroyed back to the main limbs. Coconuts, even at the water's edge, sapodilloes, alligator pears, etc., were killed and of course all the crops, such as tomatoes, peppers, eggplants, etc. The orange trees shed their leaves, but, strangely enough, were not otherwise harmed then. "They budded out again just in time to be killed by the February freeze."

On February 9th, after two or three weeks of rain, the temperature went down to 34° F. at salt water. Official record for Fort Myers for this date is 30° F. This time the fishes fared better though many of them, numbed, drifted ashore and died. Except for the almost total destruction of the citrus groves the island vegetation (what was left of it after the December freeze) escaped with negligible damage.

1898. On January 3rd, 1898, the temperature on the island ran as low as 26° F. according to some witnesses (Fort Myers official, 28° F.), and much of the vegetation, including all the crops, was ruined. Except for the (1904) 1905 cold, there has been none so killing to vegetation since. As might be expected, the mortality among fishes was high, particularly among shallow water forms. Jacks and snappers especially, also gaff-topsail cats, cowfish, turbot (a species of filefish), snook, and eels were washed up in considerable numbers, dead or dying. A few amberjacks (Florida east coast fishes, uncommon around Sanibel) were identified among the casualties. With little effort the island farmers picked up many wagonloads of fishes which they hauled and buried for compost, or fertilizer—a gift not to be scorned, but small comfort in the face of blackened crops.

1899. On February 14th, 1899, the official Fort Myers temperature was 28° F. On Sanibel it ranged near freezing, damaging crops somewhat and numbing but not killing many fishes.

(1904) 1905. The double date is given because Sanibel folk stoutly contend that the freeze was in 1904, though the nearest Fort Myers date is in 1905. Possibly both are correct for "... temperature differences of 10° F. and even more have been observed between places only a few miles apart" (Bennett, '33). On Sanibel it was a dry cold of 30° F. at salt water. Fort Myers temperatures were 27° on January 26th and 29° on the 27th. Crops and island vegetation were very seriously injured. The smaller fishes including the needlefish were the greatest sufferers. On the whole this cold was more damaging to plants than to fishes.

1917. Sanibel thermometers registered 29° to 30° F. on February 3-4, 1917, while in Fort Myers the lowest reading was 27° F. All through January there had been frosts and near freezing temperatures with very little sunshine. During this time the vegetation suffered and the freeze about finished it. This "most rawhiding cold for a man" was even harder on the fishes. Countless numbed snappers "washed into potholes and hung in the tide" while "the current lined them up in rows" in the creeks. These are narrow

irregular salt water channels winding between the countless mangrove islets which occur along part of the protected or bay side of the island. A great deal of commercial as well as sport fishing is done in the creeks. The fish houses were offering four cents a pound for snook and fishermen had no trouble making hauls of 400 to over 1000 pounds per boat, securing the helpless fishes by means of dipnets. Many numbed grouper also ended up at the fish houses. Everywhere quantities of paralyzed and dead fishes washed ashore and soon "the stench on our beaches was awful."

1928. Again Sanibel and Fort Myers do not agree as to date, but again both may be right. Dr. Perry's notes give the night of January 15-16, 1928, while the only Fort Myers low for the year (30° F.) occurred January 4th. Sanibel temperatures declined suddenly from 70° to 32.5° F. in the early morning. A stiff "nor'wester" was blowing. By daylight numbed fishes were everywhere. Fishermen made from \$20 to \$25 a day graining them. A "pair of grains" is a sort of two pronged spear. Many fishes were killed outright and they and the helpless ones were soon washed ashore. Dr. Perry records that on a quarter of a mile of bay beach over 35 species were counted including many catfish, snook, trunkfish, skipjacks, blue runners, and sand perch; a few grouper, permit, sailor's choice, toadfish, puffers, black angel-fish, snakefish, mullet, silver mullet, mangrove snappers, redfish, flounders, turbot, porcupine fish, trout, sheephead, yellow jacks, ladyfish, pompano, needlefish, hound minnows, shark suckers, yellow mouth grunts, black grunts, and sand sharks. "Large grouper and jewfish were so numbed that numbers were taken without attempt at escape." Comparatively little damage was done to crops because the wind was high, so the frost did not get at them.

1934. The suddenness of this latest freeze probably explains why so many sheephead and mangrove snappers were rendered helpless. After a warm spell (the average for October had been 78.3° F. and for November 70° F. at Fort Myers), the temperature dropped to 30° F. at salt water within a few hours (28° F. in the interior of the island) with a Fort Myers reading of 29° F. for December 12th, 1934. Calm weather and a consequent heavy frost caused great damage to vegetation. Many coconut palms even at the salt water were killed and practically all the nuts were soured; vegetable crops were ruined though the citrus trees were almost unharmed. As far as the fishes were concerned this was one of the least severe freezes. Plenty were paralyzed but lack of wind saved most from washing ashore. However a few dead and some helpless fishes came in, mostly on the bay side. These included besides sheephead and snappers a fair number of grouper, redfish, trout, catfish, jacks, snook, and a good many silver mullet. Many fishes came drifting down out of the river and creeks. On the Gulf beach the few stranded were largely jacks. Fishermen from boats dipped up 2270 pounds of mangrove snappers from the creeks alone. Most were merely numbed. Thus though it was not considered a severe freeze many thousands of fishes

died. By the second day those that had not been beached or caught were "coming alive."

Specific data can be given for the killing of young tarpon. One hundred yards inland from the Gulf, Dr. Perry has a small brackish pond, shallow and landlocked save at extreme high tides in heavy storms. Besides brackish water species the young of redfish, snook, and particularly of mullet and tarpon live and are protected in this "nursery." The pond had not been open to the Gulf in two years hence the young fishes had reached good size. After the freeze on a strip of shore only 100 feet long 68 young tarpon 14 to 24 inches long were found dead. The other inhabitants survived. We assisted at a careful seining of the pond in March, 1935 (there had been no storm tides since the freeze so the pond had remained landlocked), and did not secure a single tarpon.

GENERAL OBSERVATIONS

We could get no evidence of damage by low temperatures to marine invertebrates which are of course very abundant in the Sanibel region.

Fishing is apt to be "poor" for a few weeks after a freeze. Aside from actual casualties doubtless great numbers of the fishes able to do so leave their normal stations for a more comfortable environment. The fishermen take it as a matter of course that within two or three weeks—seldom longer—the fishes will be back, with recruits, and fishing will again be "good." That fishes migrate to escape unpleasant conditions is borne out by the experience of the past winter (1935–1936). Throughout December, January and February the weather was unusually cold, windy and disagreeable though there were no freezing temperatures and no destruction of fishes. Not only was the sport fishing highly disappointing—an indisposition on the part of the fishes to bite could account for this—but the commercial seine and net fishing was equally poor—the fishes just weren't there. With pleasanter weather the fishes returned.

The 1886 freeze appears to have been the most severe both to fishes and vegetation. In mortality among fishes the 1894 freeze ranks second followed by those of 1898, 1917, and 1928 in that order with the damage from those of 1895, 1899, (1904) 1905, and 1934 comparatively slight. For vegetation and crops the 1898 follows the 1886 freeze in severity; then come the 1894, 1934, (1904) 1905, and 1917, with the 1899 and 1928 freezes causing the slightest loss while that of 1895, generally negligible in its effects, was the only freeze to ruin the citrus groves. If the freezes are listed according to minimum air temperatures the order again differs as shown in the table. Some of the reasons for these variations in severity will be treated in the next section.

TABLE I. *Showing temperatures and relative damage caused by freezes at Sanibel Island, Florida, 1886-1934*

Order of Severity	Air Temperatures F.	Greatest Damage to	
		Fishes	Vegetation
1.	1886 ?°	1886	1886
2.	1898 26°	1894	1898
3.	1894 28°	1898	1894
4.	1917 29°	1917	1934
5.	(1904) 1905 30°	1928	(1904) 1905
6.	1934 30°	1895 (slight)	1917
7.	1899 32°	1899	1899 (slight)
8.	1928 32.5°	(1904) 1905	1928
9.	1895 34°	1934	1895 citrus only

DISCUSSION

It is quite obvious that for these nine freezes we are not dealing with the simple situation of low temperatures directly killing fishes and vegetation. Many factors in combination control the amount of damage.

In the first place Sanibel is on the northern fringe of the true tropical zone as evidenced by the presence of such trees as the gumbo-limbo, joe-wood, and the coconut palm, along with the mangroves, sea grape, buttonwood, live oak, and the palmettoes (Howell, '32). Many Sanibel fishes are at or near the northern limit of distribution for the species. Again, though a species ranges much farther northward, individuals may have become acclimated to the semi-tropics and so sensitive to unusual temperature drops. Still others would react to sudden chilling anywhere. Even among fishes in the temperate zone according to J. R. Norman ('31) "the range of temperature in which the average fish can live in comfort is comparatively limited, about 12° to 15° F. for most species." He points out however that "the power of resistance to heat and cold varies considerably in different fishes." We have no water temperatures for any of the freezes but certainly there would be none near 32° F. But to all but the hardiest fish a water temperature at Sanibel below say 60° F. might cause trouble. So we have among the fishes and subtropical plants many species unable to cope with cold and Sanibel's location so near the zonal border line insures a periodic, infrequent exposure to harsh conditions.

Sudden freezes tend to cause more widespread damage to fishes. At the beginning of a "nor'wester" the air temperature may drop as much as 20° F. in ten minutes (Patterson, '26). As shown in the 1928 freeze the overnight fall at Sanibel was from 70° to 32.5° F. with great damage resulting though the minimum temperature was well above that of many less destructive freezes. When cold comes on gradually some fishes can withstand it better while others have a chance to get to warmer water.

The water surrounding Sanibel is all shallow; none of the channels have water over 20 feet deep. Grass flats and sand bars are everywhere, with the water varying from one to six feet over them. The 10 fathom (60 foot) line is nowhere nearer than 20 miles from shore. Shallow water of course can be chilled more quickly than deep water.

Though the tide range is slight, the mean rise and fall being less than two feet, because of the great extent of the bays inside, San Carlos Bay, Pine Island Sound, Matlacha Pass, and the Caloosahatchee (which for 20 miles is really a narrow bay), there are very strong currents especially through the passes at each end of the island leading to the Gulf.

Because of the shallow water both in the bays and in the Gulf, wind can overcome the effects of tide and current and can in fact reverse them. Since wind and tide can combine to lower the water in areas already shallow—an off shore wind has been known to lower the water four feet below the plane of reference—the chilling process can thus be greatly speeded. Or if the water is held back even a severe air temperature may cause little damage to the fishes. And if the warmer Gulf water floods in all the fishes may be spared.

Any wind will help to chill the water but a high wind especially working against a strong tide will churn the water thus cooling it off more quickly. A dead calm may help to save the fishes though it may let the frost ruin the vegetation.

When the fishes become numbed, if the cold has not killed them outright, wind and tide can seal their doom by bringing them ashore or stranding them on exposed grass flats and bars or can save them by keeping them afloat till they warm up.

As mentioned above many fishes doubtless migrate as soon as the water starts chilling. But others do not or cannot. For instance because surface temperatures drop fastest and lowest the surface fishes are probably often paralyzed before they can react. Hence the high mortality among needlefish and hound minnows. So the station and habits of the fishes must be considered in an estimate of their vulnerability.

It is impossible on the basis of the material at hand to state dogmatically which species of fishes are "hardy" and which are not. Bearing in mind the factors mentioned above we can only draw general conclusions from the numbers killed against their probable local abundance on a given date.

Since winter is the dry season—the average monthly precipitation at Fort Myers, 1851 to 1930 for November to February inclusive, is only 2.05 inches (Bennett, '33)—we do not feel that variations in the salinity of the water due to rainfall or sunshine can be a factor as far as Sanibel fishes are concerned. Only in the 1895 freeze mild both as to temperature and damage *is there a record of any amount of rainfall preceding a freeze.* The fishes *that come floating down to the island from the fresh water of the upper Caloosahatchee after a cold snap* are not properly within our province.

TABLE II. *Popular and scientific names of fishes reported killed by "freezes" at Sanibel, Florida*

Scientific Name	Local Name	Names Common Elsewhere
<i>Seriola</i> sp.	amberjack	amberjack
<i>Chaetodipterus faber</i> (Broussonet)	angelfish, black	spadefish
<i>Spheroides spengleri</i> (Bloch)	blowfish; puffer	balloonfish
<i>Pomatomus saltatrix</i> (Linnaeus)	bluefish	bluefish
<i>Lactophrys tricornis</i> (Linnaeus)	cowfish	horned trunkfish
<i>Galeichthys milberti</i> (Cuvier & Valenciennes)	catfish	sea catfish
<i>Felichthys felis</i> (Linnaeus)	catfish, gaff-topsail	gaff-topsail catfish
<i>Mystriophis intertinctus</i> (Richardson)	eel, brown-spotted	snake eel
many sp., several families	flounder	flatfish; flounder
<i>Mycteroperca bonaci</i> (Poey)	grouper, black	marbled rockfish
<i>Epinephelus morio</i> (Cuvier & Valenciennes)	grouper, red	red grouper
<i>Haemulon plumieri</i> (Lacépède)	grunt, black	common grunt
<i>Orthopristis</i> sp.	grunt, yellow mouth	pigfish; grunt
<i>Hyporhamphus unifasciatus</i> (Ranzani)	hound minnow	halfbeak; ballyhoo
<i>Caranx hippos</i> (Linnaeus)	jack	crevallé; cavally
<i>Oligoplites saurus</i> (Bloch & Schneider)	jack, yellow; leather-jack	leatherjack
<i>Garrupa nigrita</i> (Holbrook); <i>Promicrops itaiara</i> (Lichtenstein)	jewfish	jewfish; giant sea bass
<i>Elops saurus</i> (Linnaeus)	ladyfish	bonyfish; ten-pounder
<i>Scomberomorus maculatus</i> (Mitchill)	mackerel	spanish mackerel
<i>Mugil cephalus</i> Linnaeus	mullet	striped mullet
<i>Mugil curema</i> Cuvier & Valenciennes	mullet, silver	white mullet
<i>Strongylura notata</i> (Poey)	needlefish	gar; needlefish
<i>Menticirrhus</i> sp.	perch, sand	sea mink; whiting
<i>Trachinotus falcatus</i> (Linnaeus)	permit	round pompano
<i>Lagodon rhomboides</i> (Linnaeus)	pinfish	bream; pinfish
<i>Trachinotus carolinus</i> (Linnaeus)	pompano	pámpano; pompano
<i>Chilomycterus schoepfii</i> (Walbaum)	porcupine fish	balloonfish; spiny boxfish
<i>Spheroides spengleri</i> (Bloch)	puffer; blowfish	balloonfish; swellfish
<i>Sciaenops ocellatus</i> (Linnaeus)	redfish	channel bass
<i>Caranx crysos</i> (Mitchill)	runner, blue	hard-tailed jack
<i>Orthopristis chrysopterus</i> (Linnaeus)	sailor's choice; pigfish; grunt	pigfish, etc.
<i>Carcharinus</i> sp.; <i>Carcharias</i> sp.	shark	shark
<i>Sphyrna zygaena</i> (Linnaeus)	shark, hammerhead	hammerhead shark
<i>Scoliodon terraenovae</i> (Richardson)	shark, sharp nose	sharp-nosed shark
<i>Sphyrna tiburo</i> (Linnaeus)	shark, shovel nose	shovel-nosed; bonnet shark
<i>Echeneis naucrates</i> Linnaeus	shark sucker	remora; shark-sucker
<i>Archosargus probatocephalus</i> (Walbaum)	sheephead	sheepshead; prisoner fish
<i>Caranx</i> sp.	skip-jack	skip-jack
<i>Synodus foetens</i> (Linnaeus)	snakefish	lizard fish
<i>Lutianus griseus</i> (Linnaeus)	snapper, mangrove	gray snapper
<i>Centropomis undecimalis</i> (Bloch)	snook	rovalia; robalo
<i>Lutianus synagris</i> (Linnaeus)	spot, red (young Lane snapper)	spot snapper
<i>Tarpon atlanticus</i> (Cuvier & Valenciennes)	tarpon	tarpon, tarpum
<i>Opsanus tau</i> (Linnaeus)	toadfish	bull-dog fish; scorpion
<i>Ogocephalus radiatus</i> (Mitchill)	toad, rock	batfish
<i>Cynoscion nebulosus</i> (Cuvier & Valenciennes)	trout	trout; spotted squeeteague
<i>Lactophrys</i> sp.	trunkfish	trunkfish; boxfish
<i>Balistes carolinensis</i> Gmelin	turbot	filefish; triggerfish

CONCLUSION

In the last analysis the effect of a "freeze" on the fishes in the region of Sanibel Island, Florida, is determined primarily by the suddenness and amount of the fall, the minimum temperature attained, and the duration of the cold. Various factors, however, modify the effects of the temperature conditions; and of these the more important are the velocity and direction of the wind, and the stage and range of the tide.

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A COMPARISON OF ROOTS OF SOUTHERN SHORLEAF PINE IN THREE SOILS

LEWIS M. TURNER

University of Arkansas, Fayetteville, Arkansas

In the field of forest ecology a problem exists in correlating site values, or site indices, with the features of soils that are influential in the determination of the site indices. Further, of interest and value, is knowledge of the gross morphology of the root system, whose character is influenced greatly by the features of the soil, not disregarding, of course, the inherent tendencies of the plant itself. It is apparent that information on the performance of roots of given species, in different soils affording certain site values, would promote an understanding of the site requirements or preferences of these species. It is the purpose of this study to compare, in a quantitative way, the root system of southern shortleaf pine, *Pinus echinata* Miller, in three Arkansas soils of known site value for the species.

REVIEW OF LITERATURE

General studies of seedling and mature tree roots

Nobbe (1875), Barker ('20), Peren ('23), Adams ('28), Gemmer ('28), Toumey ('29), Clements, Weaver and Hanson ('29), and Pessin ('35) have conducted studies of the form, or relation of competition to form, of root systems of seedlings or young trees. Cannon ('11), Peren ('23), Baker ('25), Roberts ('27), Swarbrick and Roberts ('27), and Cheney (1928-29) have made general studies of, or have referred to, the form of root system of mature desert plants, fruit or forest trees.

Studies of the relation of soil factors to the root system of tree seedlings

Schwarz (1892) found that the total length of roots of one-year-old pine seedlings decreases with increasing concentration of the soil solution. Clements, Weaver and Hanson ('29) studied the relationship of root-system form to success in competition with grasses. Magyar ('29) investigated the form and extent of root systems of deciduous tree seedlings under nursery conditions. Wahlenberg ('29) influenced root development of western yellow pine seedlings at various levels by varying the position of fertile and non-fertile soil layers. Holch ('31), working with seedlings of five deciduous species, found that although form of root system seemed hereditary with the species, this was more or less correlated with moisture conditions in sites usually occupied by the species.

Studies of the relationship of soil factors to the root system of mature trees

Sampson ('14, '17) has reported on the root system of range plants. Korstian ('17) studied the roots of forest trees in relation to the problem of plant indicators of soil moisture conditions. Pulling's investigations ('18) in the northern edge of the tree belt in Canada, led him to conclude that the root system of *Picea mariana*, *Larix laricina*, and *Betula papyrifera* is shallow, and that of *Pinus banksiana* and *Pinus strobus* deep, habits which are rigidly adhered to by these species. *Picea glauca* has a shallow, and *Populus balsamifera* a deep root system, but these species are more flexible in their root habit. He believed that degree of flexibility, as regards soil penetration, may determine the northern distribution of many plants. Aaltonen ('20), in investigating root competition in stands of different ages and different sites, found that the roots of trees were more numerous on poorer soils, and that they extended farther, both horizontally and vertically, in poor soils than in good. Kokkonen ('23) investigated the root system of *Pinus sylvestris* in drained moors. Hesselink ('26) and Schreiber ('26) made comparative studies of the relation of extent of root system to the number of growing tips of several tree species. Weaver's studies ('19) included some observations on the form and extent of the root system of *Pinus flexilis* and *Picea engelmanni*. Hilf ('27) investigated the form of the root system of Norway and Scotch pine and beech, and found that good, fine sandy forest soils produced a well developed tap root with numerous laterals, lime soils produced stunted root systems. On the best soils, the lateral roots were much branched, while grassy, *Vaccinium* sites produced shorter roots. In general poorest sites produced long roots with few branches. Laitakari ('27) studied the root system of Scotch pine, to lesser extent the root systems of Norway spruce and birch. He found that the total length of the roots varies according to the nature and fertility of the soil. Most widely spread roots occur in sandy soil, the least in stony, moranic soil. Clay soil and moraine soil without stone are intermediate. The shallowest root systems occurred in sandy soil, and the deepest in better soils. Vater ('27) concluded that the common belief that *Picea excelsa* is always shallow rooted, *Pinus sylvestris* deep rooted, and *Fagus sylvatica* medium, is erroneous. He believed that much could be learned of the exact nature of root systems of trees by digging. Stevens ('31) found that the roots of young white pine trees grew approximately twice as much on sandy as in clayey soils.

METHOD OF STUDY

In 1934 (Turner, '36) and 1935, 165 plots in five counties in Arkansas, were studied to determine the relation of rate of growth of pine with certain site features. On each plot two trenches were dug to determine the character of the soil and to make observations on the nature of root size and distribution in the soil profile. Each trench, four feet long by at least three feet deep, was

dug three feet from the base of a dominant tree and at right angles to radii emanating from the base of the tree.

The face of the trench nearest the tree was examined carefully and the size and position of every severed root marked on a scaled diagram. Roots were arbitrarily grouped in six classes, those nearest 4, 3, 2, or 1 in. between $\frac{1}{4}$ and $\frac{3}{4}$ in., and less than $\frac{1}{4}$ in. in diameter. Obviously most roots so marked were of the dominant tree near to which the trench was dug, but it is recognized, of course, that roots of adjacent trees were encountered. Hence, the record is of the roots of a dominant tree to a depth of three feet in a segment four feet long, three feet from the tree, plus any roots of other trees that happen to occur within the plane of the trench face. This affords a workable basis for comparative purposes, but is, of course, ineffective as an absolute measure of the magnitude of root systems.

From the number of records secured, forty-five were selected which pertain to fifty-year-old, pure stands of southern shortleaf pine. The records of these plots were divided equally among three soil types, fifteen on Caddo silt loam, slope 1 per cent; fifteen on Susquehanna fine sandy loam, slope 9 per cent; and as many on Hanceville fine sandy loam, slope 25 per cent. The fifteen records, each, for the three soils were superimposed on a single sheet (figs. 1, 2 and 3).

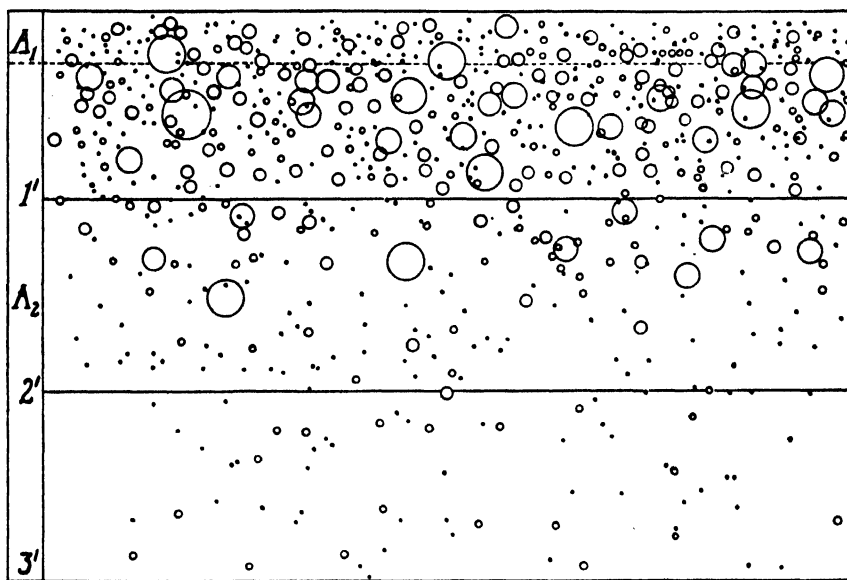


FIG. 1. Roots of 50 year old *Pinus echinata* trees in fifteen trench faces in Caddo silt loam.

Table I is a summary of the occurrence of roots of various sizes at various depths in the soil profile in the three soils. To make a more comprehensive and accurate comparison of the distribution of the roots at different depths, the profile was divided into four horizontal divisions, or layers (0-9, 9-18,

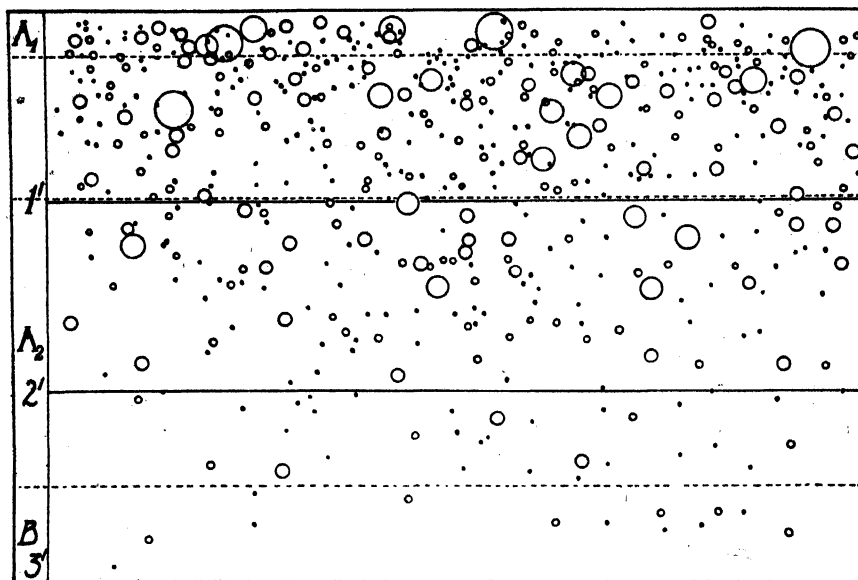


FIG. 2. Roots of 50 year old *Pinus echinata* trees in fifteen trench faces in Hanceville fine sandy loam.

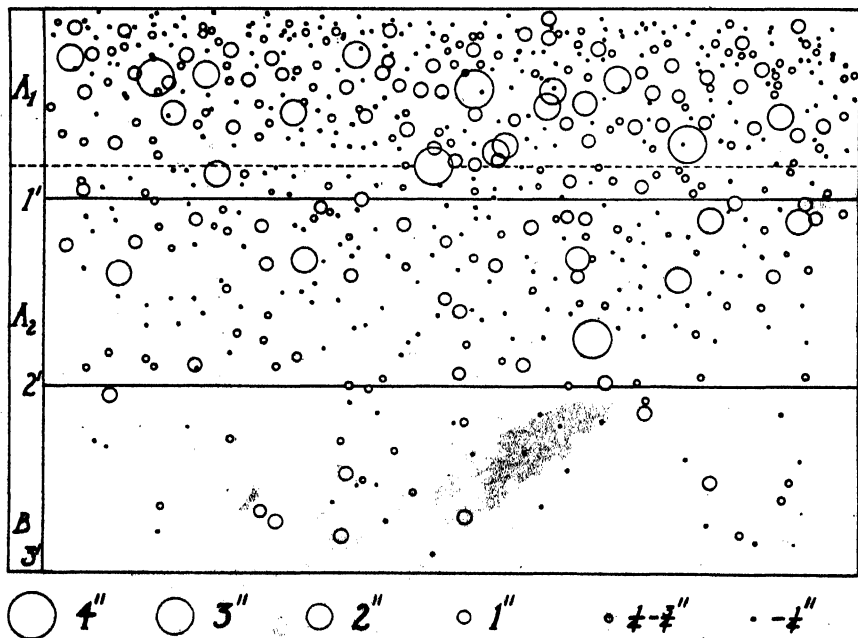


FIG. 3. Roots of 50 year old *Pinus echinata* trees in fifteen trench faces in Susquehanna fine sandy loam.

TABLE I. *Tabular summary of root distribution of fifty-year-old shortleaf pine trees on trench faces in three soils*

Level inches	Roots 4 in. in diam.		Roots 3 in. in diam.		Roots 2 in. in diam.		Roots 1 in. in diam.		Roots ½–¾ in. in diam.		Roots ¼ in. in diam.		Total cross-sec. area* of roots per layer over ¼ in. in diam.
	No.	Area*	No.	Area	No.	Area	No.	Area	No.	Area	No.	Area	
Hanceville fine sandy loam													
0-9	0	0	4	22.28	10	31.40	39	30.81	65	13.0†	155		103.49
9-18	0	0	0	0	7	21.98	21	16.59	37	7.4	72		45.97
18-27	0	0	0	0	0	0	7	5.53	16	3.2	41		8.73
27-36	0	0	0	0	0	0	2	1.58	7	1.4	17		2.98
Totals	0	0	4	22.28	17	53.38	69	54.51	125	25.0	285		161.17
Caddo silt loam													
0-9	1	12.57	6	42.42	20	62.80	69	54.51	74	14.8	204		187.10
9-18	0	0	3	21.21	8	25.12	28	22.12	46	9.2	86		77.65
18-27	0	0	0	0	0	0	4	3.16	14	2.8	68		5.96
27-36	0	0	0	0	0	0	0	0	12	2.4	28		2.40
Totals	1	12.57	9	63.63	28	87.92	101	79.79	146	29.2	386		273.11
Susquehanna fine sandy loam													
0-9	0	0	3	21.21	12	37.68	48	37.92	74	14.8	204		111.61
9-18	0	0	1	7.07	7	21.98	25	19.75	47	9.4	78		58.20
18-27	0	0	1	7.07	0	0	8	6.32	25	5.0	43		18.39
27-36	0	0	0	0	0	0	6	4.74	9	1.8	16		6.54
Totals	0	0	5	35.35	19	59.66	87	68.73	155	31.0	314		194.74

* Cross-sectional area of severed roots in square inches

† Calculated on the basis of .5 in. diameter

18-27, and 27-36 inches) and the number of roots of each size counted in each layer. In addition, the cross-sectional area of all recorded roots of each size in each layer was determined of all roots above .25 in. in diameter and totalled for each layer.

SUMMARY OF DATA

Of the three soils (see table I) Caddo silt loam had most roots of all sizes (a few less than Susquehanna f. s. l. in the .25-.75 in. class) in the described standardized soil profile. Hanceville fine sandy loam had the fewest roots, and Susquehanna fine sandy loam was intermediate in this respect.

Caddo silt loam had the most large roots (in the 2, 3 and 4 inch classes), Hanceville fine sandy loam the fewest, and Susquehanna was intermediate.

This numerical advantage, and actual greater cross-sectional area in the soil profile, was not as marked in the smaller root classes, that is, the roots 1 in. in diameter or smaller.

Caddo silt loam and Hanceville fine sandy loam had a conspicuously larger number of roots in the two upper layers (0-18 in.), being 96.7 per cent and 92.5 per cent, respectively, of the total cross-sectional area of all roots in the profile. Susquehanna fine sandy loam contained only 87.1 per cent of the total cross-sectional area of all roots in the two upper layers. The greater cross-sectional area of roots in the upper layers in the first two soils was due largely to the greater number of large roots.

Caddo silt loam had more smaller roots in the two lower levels (18-36 in.) than the other soils. This was also the condition in the two upper levels of Caddo silt loam, but it was less marked there.

The clay subsoils of both Hanceville and Susquehanna fine sandy loam were occupied by medium sized roots to greater extent than the high silt content subsoil of Caddo silt loam, but there was apparently less branching and hence fewer small roots in the former soils.

DISCUSSION OF RESULTS

Caddo silt loam, Susquehanna fine sandy loam, and Hanceville fine sandy loam (Nelson, Sachs and Austin, '23) were selected for this comparative study because they afford nearly the best, intermediate, and nearly the worst edaphic situations for the growth of the species in question (Turner, '36). Dominant and codominant fifty-year-old trees on Caddo, Susquehanna and Hanceville soil were 90 ft. tall and 13 in. in diameter, 73 ft. tall and 12 in. in diameter, and 45 ft. tall and 11 in. in diameter, respectively. Table II summarizes some of the physical characteristics of these soils.

Hanceville fine sandy loam is a soil of the Ouachita mountain region with slope varying from little to 60 per cent or more. The plots selected for this study were all on sites with slope near 25 per cent. The A₁ horizon, 0-3 in.,

TABLE II. *Depth of horizons, and physical and electrometric analysis of Caddo silt loam and Susquehanna and Hanceville fine sandy loams*

Soil	Horizon	Depth of horizon in inches	Sand	Silt	Colloid	pH	Site index for <i>Pinus echinata</i>
Hanceville fine sandy loam. Slope 25%	A ₁	0-3	57	18	25	6.0	45
	A ₂	3-12	48	15	37	5.0	
	B	12-30	46	14	40	4.8	
Susquehanna fine sandy loam. Slope 9%	A ₁	0-10	66	15	19	5.4	73
	A ₂	10-37	55	13	32	5.0	
	B	37-	47	9	44	4.6	
Caddo silt loam. Slope 1%	A ₁	0-3	36	46	18	5.8	90
	A ₂	3-38	24	40	36	5.0	
	B	38-	24	39	37	5.0	

has a high sand, relatively low silt, and medium colloid content; the A_2 , 3–12 in., contains somewhat less sand and silt, and relatively high colloid content; the B horizon, 12–30 in., slightly lower silt and sand and higher colloid than the A_2 horizon. In general, the clay of the subsoil is friable. There is usually a considerable quantity of sandstone in all horizons. The site index of shortleaf pine (average height of dominant and codominant trees at fifty years of age) for this soil is 45, which is quite low for the species in Arkansas.

Susquehanna fine sandy loam is a soil of the upper coastal plain region of the state. It is usually associated with rolling topography, with slope ranging from 3 per cent to 12 per cent or more. The plots selected for this study were all in situations where the slope was near 9 per cent. The A_1 horizon, 0–10 in., has high sand and relatively low silt and colloid content; the A_2 horizon, 10–37 in., has somewhat less sand, low silt, and medium to high colloid content; the B horizon, below 37 in., has relatively high sand, low silt, and high colloid content. The clay of the subsoil is usually plastic. The site index for shortleaf pine for this soil is 73 which is medium for the species in the state.

Caddo silt loam is "flatwoods" type of soil of the lower coastal plain region of the southeastern part of the state. The slope of this soil is usually not over 2 per cent. The A_1 horizon, 0–3 in., has medium sand, high silt and low colloid content; the A_2 horizon, 3–38 in., and the B horizon, below 38 in. have relatively low sand, rather high silt, and medium colloid content. This soil is presumably loessial and recent in origin, poorly drained and its immaturity evidenced by absence of strong stratification. Of the better pine growing soils that occur in considerable area in the state, Caddo silt loam ranks high, its site index for shortleaf pine being 90.

The positive correlation of higher site index and greater cross-sectional root area of shortleaf pine in standardized soil profiles is established by this study. It is apparent that the better the site, and the larger the trees growing there, of a given age, the greater the number and size of roots. In brief, a soil which affords the fastest height growth, Caddo silt loam, has more roots, particularly more large roots, than any of the three soils; Hanceville, the poorest soil as regards rate of height growth, the least; Susquehanna, with an intermediate site index, is also intermediate as regards number and size of roots. This is opposed to Aaltonen's conclusions ('20) and in agreement with Hilf ('27), Holch ('31) and possibly with Laitakari ('27). The difficulty in comparing results and conclusions lies in the ambiguity in defining "good," and "poor" forest soils.

The relatively larger percentage of cross-sectional area of roots (96.7) in the two upper levels (0–18 in.) in the Caddo silt loam profile is doubtless associated with the fact of poorer drainage and resulting poorer aeration of the lower levels (18–36 in.) of this soil. A shallow root system in this soil type would be expected. Susquehanna fine sandy loam had the least, or only 87.1 per cent of the total cross-sectional area of roots in the two upper

levels, and Hanceville had 92.5 per cent. It is probable that the lower layers of both of these soils are much better aerated than those of Caddo silt loam. On the other hand, the presence of these relatively high percentages of roots in the lower levels of Hanceville and Susquehanna soils indicates an ability of roots of shortleaf pine to penetrate subsoils of relatively high colloidal content, in these cases both friable and plastic clays. However, more large roots and fewer small ones in the lower levels of these soils would indicate a tendency towards less branching in the heavier clayey subsoils than in those with higher silt content.

The author (Turner, '36) has pointed to the significant relationship between available water and height growth of southern pine, demonstrating that topography and the physical nature and depth of the soil horizons have a profound effect on the rate of growth of the native pines of Arkansas. In brief, up to certain limits (the overflow soils of river bottoms, and flat soils with hardpan subsoil near the surface are not suited to pine growth) the more favorable the water supply the faster is height growth. This factor apparently dominates all others, such as soil nutrient content, soil reaction, and direction of slope, within the limits within which these features obtain on pine-occupied soils. A further correlation—available soil moisture and number and size of roots of pine trees—is suggested by this study. In brief, the more satisfactory the water supply, within the described limits, the faster the height growth and the larger the number and size of roots of pine, in standardized soil profiles.

SUMMARY AND CONCLUSIONS

1. Roots of fifty-year-old southern shortleaf pine were recorded by size and position in trenches three feet deep by four feet wide, three feet from the base of, and facing a dominant tree in pure stands of the species on three soils in southern Arkansas.
2. The soil affording the highest site index, Caddo silt loam, had: (a) essentially more and larger roots in the profile, (b) conspicuously more larger roots in the upper 18 inches, and (c) more smaller roots in the lower 18 inches, than the two inferior soils.
3. Susquehanna fine sandy loam, of intermediate site value, was also intermediate in regard to number and size of roots. Hanceville fine sandy loam, with lowest site index, was also lowest in respect to the above.
4. The presence of a high percentage (96.7) of the total cross-sectional area of roots in the profile in the upper 18 inches of Caddo silt loam is presumably attributable to the flat, poorly drained nature of the soil, and resulting poor aeration of the lower level. Susquehanna and Hanceville fine sandy loams, have 87.1 per cent and 92.5 per cent, respectively, of the total cross-sectional area of roots in the profile in the upper 18 inches. Both of these soils have considerable slope and doubtless better aeration of their subsoil.

5. A relatively larger number of larger roots and fewer smaller ones in the subsoil of Susquehanna and Hanceville soils indicates an ability of shortleaf pine roots to penetrate both friable and plastic clays, but less tendency towards branching than occurs in Caddo with a high silt content subsoil.

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SOME CHANGES IN THE SOIL FAUNA ASSOCIATED WITH FOREST FIRES IN THE LONGLEAF PINE REGION

FRANK HEYWARD

Southern Forest Experiment Station

AND

A. N. TISSOT

Florida Agricultural Experiment Station

Forest fires are more prevalent in the longleaf pine region of the Southeast than in any other part of the United States. Most of these fires occur during the winter months. Field examination of soils on areas protected from fire for 10 years or longer and similar soils subjected to frequent fires revealed striking differences in soil structure of the topmost horizons (Heyward, '35, and Heyward and Barnette, '34). Penetrability measurements of the surface of the mineral soil showed that the soils protected from fire were considerably more penetrable than soils from burned areas. Soils unexposed to fire were likewise considerably lighter in weight per unit volume.

This paper presents data on the activity and abundance of certain of the soil-animal population of burned and unburned longleaf pine forests. It also largely explains some of the differences in the physical condition of soils from such forests.

The importance of the effect of the animal population on soil formation has long been recognized. Taylor ('35) reviews some of the more recent work on the subject of animal influences on the soil. Not only is the soil rendered more permeable because of their runways and abodes, but there is a constant mixing of surface and subsoil by the soil fauna. This constant mixing further aerates and loosens the soil, and is highly important as a means of incorporating organic matter into the soil. Bryson's work in Kansas ('31) illustrates the important influence of one animal group alone—the insects—on soil formation. This investigator points out that there were from 5.8 to 7.5 insect burrows per square foot in the region in which he was working. One of the earliest investigators to record the importance of the lesser soil animals was Darwin ('82). His interesting studies on earthworms are constantly referred to in soil literature. Müller's researches in Denmark 50 years ago further established the importance of earthworms in soil formation. As Romell ('35) states, "the rôle of earthworms in creating and maintaining a crumb mull type of humus layer has been rather generally accepted after Müller's classical studies" (1887). Indeed, the mull type of humus layer is generally recognized as being the outcome of a series of soil conditions, one of the most important of

which is earthworm activity, although Romell ('35) presents evidence that myriapods also may be instrumental in mull formation.

DESCRIPTION OF BURNED AND UNBURNED AREAS

In appearance of forest floor and ground cover marked differences are found between burned and unburned areas. On areas protected from fire for 10 years or longer two general conditions exist. Under closed stands herbaceous plants are usually totally excluded by the shading effect of the overstory and by the smothering effect of pine litter. A well-formed A_0 horizon 2 to 3 inches in thickness is typical. In openings in the forest on unburned areas dense, almost pure stands of native grasses occur. Wire grass (*Aristida* sp.) is one of the most common of these. This grass, after attaining a height of 18 to 20 inches, tends to bend over and form a tangled, interwoven mass which forms an excellent mulch over the soil. Frequently burned areas, on the other hand, are characterized by the absence of a well-formed forest floor or a dense, tangled grass cover. A vigorously growing and diversified ground cover is typical; but, because this vegetation is rarely older than 1 or 2 years, due to frequently occurring fires, the individual plants are erect instead of recumbent and afford but a poor mulch for the soil. After each winter fire, the soil is directly exposed to rain and insolation for several months. By early summer, however, the rapidly growing ground cover usually affords protection against the elements.

The soil under the forest floor on unburned areas is strikingly in contrast to soil from burned areas. The soil protected from fire is so loose and permeable that it can be scooped up with the fingers to a depth of 3 to 4 inches. Many insect remains occur. Frass of insects and arthropods is abundant and in places earthworm casts are also plentiful. Numerous holes $\frac{1}{16}$ - to $\frac{1}{8}$ -inch in diameter are present in certain soils. Larger holes and tunnels from $\frac{1}{2}$ -inch to 1 inch in diameter are frequent.

On unburned areas evidence of an active soil fauna also exists under the grass cover in openings in the forest, but to a much smaller degree than in soil underlying a well-developed A_0 horizon. Holes and tunnels of the larger animals, such as moles and mice, are much less abundant.

The soil of burned areas is compact and impenetrable. Faunal signs, such as excrement, dead animals, or burrows, are much less in evidence than on areas protected from fire.

FIELD STUDY

During field collection of samples for physical and chemical studies of soils from burned and unburned areas, notes were taken on the activity of the macrofauna. For each soil sample collected a spot approximately 8 inches square was cleared of ground cover or organic debris. Within these spots numerous holes were found. These holes were, in general, of two types, those

$\frac{1}{16}$ - to $\frac{1}{8}$ -inch in diameter and those $\frac{1}{2}$ -inch to 1 inch in diameter. Unquestionably many of the smaller holes were covered in removing the layers of organic matter; also, it is almost a certainty that many holes less than $\frac{1}{16}$ -inch in diameter were present but were not seen. For these reasons, it was obvious that a count of the smaller holes would be very inaccurate, unless much time were spent in making such an inventory. Therefore, only holes approximately $\frac{1}{2}$ -inch or more in diameter were tallied. The sample spots examined were distributed at random on plots from $\frac{1}{4}$ - to $\frac{1}{2}$ -acre in area. Table I gives the

TABLE I. *Number of animal holes and tunnels in soils on burned and unburned areas*

Area	Spots examined for each burned and unburned plot	Holes and tunnels at least $\frac{1}{2}$ -inch in diameter	
		Unburned	Burned
	Number	Number	Number
Urania, La.	80	37	7
McNeill, Miss.	80	21	1
McNeill, Miss. ¹	46	16	0
Stapleton, Ala.	88	7	1
Trenton, Fla.	35	11	1
Raiford, Fla.	35	5	0
Totals	364	97	10

¹ Densest portions of stand only.

results of these tallies for five study areas. The holes and tunnels recorded are probably those dug by beetles and small mammals such as moles and mice (fig. 1). Where holes or tunnels had become partly or completely filled in with soil from disuse, they were not tallied. Examples of these were numerous.

While collecting 80 individual soil samples from the zero to 3-inch depth of each burned and unburned area, all earthworms were tallied. For the Urania area 14 worms were found on the unburned plot as compared with 3 on the burned; for McNeill 22 were found on the unburned and 15 on the burned. For the Stapleton area the results were reversed, 4 worms being found on the unburned plot and 18 on the burned. A point worthy of mention is that the Stapleton samples were collected at the beginning of a 2-day rain. Several worms were found crawling on the soil surface of the burned plot, on which the soil was wetted sooner by the rain than the soil of the unburned, which was covered by a layer of organic matter.

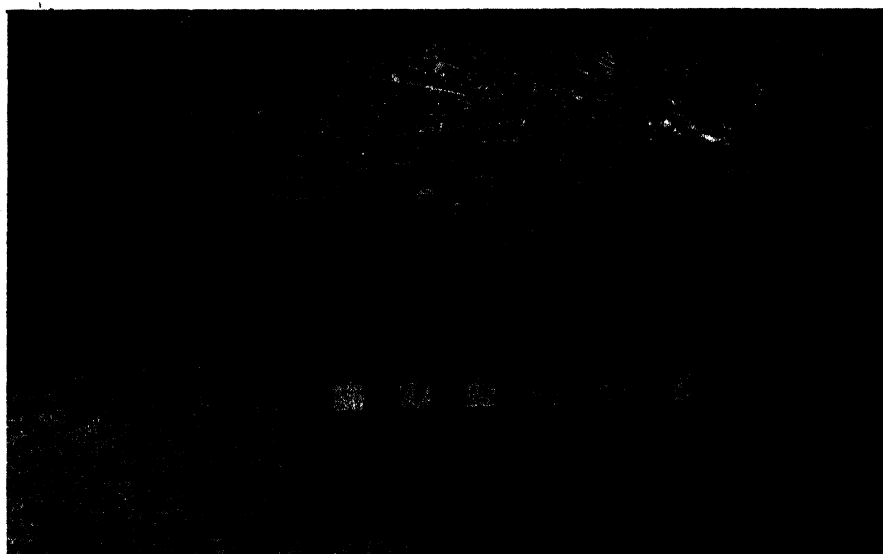
SOIL MICROFAUNA ² OF BURNED AND UNBURNED AREAS

The soil microfaunal population is of particular importance in forest soils of the region, since from field observations it appears evident that these minute animals are highly important in the breakdown of forest litter.

² The term "microfauna" is used in this paper to designate the lesser soil animals recognizable under a binocular microscope giving a magnification of 15 X.



A



B

FIG. 1. A. Holes of small animals under A_0 horizon in longleaf pine forest unburned for 11 years. B. Small animal tunnels. The scale is 12 inches long.

Differential counts were made on composite samples for burned and unburned areas as follows: At eight widely separated spots on each burned and unburned area, $\frac{1}{2}$ -square-foot individual samples were collected from the entire A_0 horizon. All herbaceous plants growing within this area were collected. Thus the comparison of burned and unburned plots resolved into a comparison of the fauna inhabiting the well-formed A_0 horizon from the unburned plots with the fauna inhabiting a miscellaneous aggregate of herbaceous

plants from the burned plots. For each spot sampled, one-fourth square foot of mineral soil to a depth of 2 inches was also collected. These samples were placed in canvas bags and shipped immediately to the laboratory, where they arrived not later than two days after collection.

The animal population was extracted from the samples of litter and ground cover by means of Berlese funnels, the animals being caught in alcohol, from which they were removed for identification as desired.

The animals were collected from the mineral soil samples from the Trenton and Adrian areas by sifting. The soil was first passed through a 2-mm. sieve. The coarse material that did not pass through was spread on a large sheet of white paper and examined for animals. The finer material that passed through was next run through a sieve with 1-mm. openings. That portion which passed through this sieve was practically pure sand and was discarded. The remainder was examined over a sheet of paper and the animals recovered. It seemed probable that many of the animals were not found in this way, therefore the technic for recovering the animals was changed. For all subsequent areas the soils were placed in Berlese funnels equipped with fine mesh sieves. The soil was first passed through a coarse $\frac{1}{8}$ -inch sieve. The debris that did not pass through was spread in a thin layer over the funnel screen and the finer soil stacked on this. The soil remained in the funnels until it was fully air-dried.

The results of animal counts for nine paired burned and unburned plots are given in tables II and III.

DISCUSSION

The observations and data presented here offer a clear explanation of the differences in penetrability and in weight per unit volume of soils on areas protected from fires as compared with soils subjected to frequent fires. The well-developed forest floor typical of dense pine stands protected from fire appears to be a highly favorable habitat for the soil fauna. This organic layer not only affords excellent cover for passageways and abodes of small mammals but also forms an excellent source of food for the soil microfauna. As a result of the diversified and abundant faunal population characteristic of unburned areas, the soils of such areas are honeycombed with animal passageways. The surface mineral soil is constantly agitated and turned over by these animals. The addition of frass and dead animal remains over a period of years is without doubt an important factor in profile development as well as from the standpoint of fertility.

Soils on areas subjected to frequent fires lack the porosity and high degree of penetrability exhibited by soils protected from fire. This may be attributed largely to a much less numerous and less active soil fauna. However, the mere presence of an organic cover, such as the A_0 horizon of unburned soils, would do much toward preventing a compacting of soil by insolation and the impact of driving rains characteristic of the region. That soils subjected to frequent fires lack such a cover is obvious.

TABLE II. *Soil microfauna from burned and unburned areas*³

Animals	Unburned		Burned	
	A ₀ horizon	0-2" mineral soil	Ground cover	0-2" mineral soil
	Number	Number	Number	Number
<i>Acarina</i> (mites) ⁴	5,415	4,719	1,107	143
<i>Acarina</i> (ticks)	2	0	0	0
<i>Araneida</i> (spiders)	41	5	12	2
<i>Chernetidia</i> (pseudoscorpions)	4	0	2	3
<i>Thysaneura</i> (bristletails)	4	46	2	4
<i>Protura</i>	0	1	0	1
<i>Collembola</i> (springtails)	1,092	10	188	3
<i>Orthoptera</i> (roaches)	3	1	0	1
<i>Isoptera</i> (termites)	16	2	0	0
<i>Psocoptera</i> (psocids)	20	0	16	1
<i>Thysanoptera</i> (thrips)	310	0	65	1
<i>Hemiptera</i> (true bugs)	21	3	19	0
<i>Lepidoptera</i> (moths)	1	0	1	1
<i>Coleoptera</i> (beetles)	48	17	16	10
<i>Coleoptera</i> (larvae)	45	39	18	20
<i>Hymenoptera</i> (ants, mostly)	350	136	53	240
<i>Diptera</i> (two-winged flies)	75	51	31	15
<i>Insecta</i> (larvae and pupae, order undetermined)	100	0	6	0
<i>Isopoda</i> (pill-bugs)	2	1	0	0
<i>Chilopoda</i> (centipedes)	15	5	0	0
<i>Diplopoda</i> (millipedes)	5	2	0	3
<i>Annelida</i> (earthworms)	6	52	3	13
<i>Mollusca</i> (snails)	1	0	0	0

³ Figures based on 4 sq. ft. of A₀ horizon or ground cover and 2 sq. ft. mineral soil except those for Trenton and Adrian areas, which are based on 3 and 1½ sq. ft., respectively.

⁴ Number of mites estimated by means of a sampling device consisting of a glass dish with 25 ruled squares each, 1 cm. on a side.

TABLE III. *Total soil microfauna for individual study areas*

Study Areas	Unburned		Burned	
	A ₀ horizon	0-2" mineral soil	Ground cover	0-2" mineral soil
Trenton, Fla.	4,019	30	36	20
Adrian, Ga.	134	0	25	1
Urania, La.	220	181	90	192
McNeill, Miss.	1,281	3,783	103	78
Stapleton, Ala.	830	906	913	83
Mt. Dora, Fla.	86	9	0	0
Bartow, Fla.	53	16	15	14
Lake Butler, Fla.	182	31	256	46
Raiford, Fla.	771	134	101	27
Totals	7,576	5,090	1,539	461

It is noteworthy from the preceding data that, with but few exceptions, the same microfaunal species occurred on both classes of soil; there was, however, a large difference in total number of organisms. Approximately five times as many animals occurred in the A_0 horizon as in the ground cover and approximately eleven times as many animals in soil from unburned plots as in soil from the burned plots. It is noteworthy that four times the number of annelids (earthworms) were found in the soil from unburned plots as compared with soil from burned. The greater number of centipedes on the unburned area is doubtless due to the greater population of other animals, the centipedes being predacious in feeding habit. Lastly, the predominance of mites over all other animals in soil from both burned and unburned plots is outstanding. The percentage of mites to total number of animals was as follows: 71 percent for the A_0 horizon, 93 percent for the 0-2 inches of unburned soil, 72 percent for ground cover, and 31 percent for the 0-2 inches of soil from burned areas.

Many of the micro-soil animals are extremely sensitive to desiccation. The absence of animals in the burned samples from Adrian and Mt. Dora was doubtless due to the dry condition of the soil when sampled in the field. Since the A_0 horizon of unburned areas forms a good mulch on the soil surface, it is evident that moisture, as well as food conditions, is more favorable to the microfauna than the corresponding conditions in the soil of burned areas.

The importance of earthworms and arthropods in mull formation has been mentioned previously. Bornebusch ('30) states that worms mix organic matter and mineral soil, whereas arthropods break down vegetable materials and transform these into humus. From the preceding data it is seen that both earthworms and arthropods were abundant in the soils of unburned areas. Bornebusch points out that earthworms are typical of mull humus layers, whereas arthropods are more typical of mor layers. The occurrence of both groups of animals in the same soil would indicate a humus layer intermediate in characteristics between mull and mor.⁵ These animals unquestionably tend to create favorable physical soil conditions; but, in a region characterized by rapid decomposition of organic matter, such as the longleaf pine region, it is not so obvious that the soil microfauna increases organic matter within the mineral soil. The well-aerated condition of the soil, brought about largely by the fauna, would tend to accelerate organic decomposition.

It would seem, in the longleaf pine region where the greater percentage of the forest lands are burned over annually, that small animals incapable of rapid locomotion would all be killed by fires. This would mean that areas burned annually would be destitute of such animals. Study of the behavior of forest fires in the longleaf pine region by Heyward have revealed that even very hot surface fires rarely heat the underlying soil to more than 80°

⁵ That this is actually the condition of the humus layer found under long-unburned stands of pine in the longleaf region will be reported in a later publication in which the principal characteristics of this type of humus layer will be described.

to 90° C. at a depth greater than ¼-inch below the surface. Moreover, such fires, particularly where occurring annually, generally leave small clumps of vegetation untouched. If, then, the soil microfauna of such localized spots were unharmed and if either the animals themselves or their eggs were only ¼- to ½-inch beneath the soil surface, they would stand an excellent chance of escaping harm during the fire. The entire area might then be repopulated by these individuals.

SUMMARY

Observations of animal signs and counts of the microfauna show that the A₀ horizon of soils supporting dense, long-unburned longleaf pine forests offers an excellent habitat for a diversified soil fauna. This is in contrast with pine forests subjected to frequent fires in which, instead of an A₀ horizon, a ground cover of herbaceous plants is present.

Soils of unburned areas were riddled with holes and tunnels of small mammals and insects, a condition generally lacking on frequently burned areas.

The A₀ horizon of unburned areas contained approximately five times as many microfaunal forms as the ground cover of burned areas. The top 2 inches of mineral soil of unburned areas contained eleven times more such animals than the corresponding soil depth from burned areas.

In general, the same microfaunal groups were found in soils protected from fire as in soils exposed to periodic fires, although the total number in each was different.

In general, earthworms were more numerous in soils from unburned areas.

Mites were by far the most abundant group of microfauna, 93 percent of the animals in the soil from unburned areas belonging to this group.

The diversified active soil fauna of the unburned areas is believed to be responsible for the penetrable and well-aerated soil typical of such areas. This is in striking contrast to the more compact, less porous soil of frequently burned areas in which animal activity is much less abundant.

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GERMINATION BEHAVIOR OF SOME CALIFORNIA PLANTS

N. T. MIROV

California Forest and Range Experiment Station, Berkeley, California

It is a matter of everyday observation that seeds of various plants behave differently when placed under conditions which are ordinarily considered to be favorable to germination (*i.e.* appropriate temperature and moisture). Some germinate readily while others do not.

The causes of failure to germinate have been summarized by Crocker ('16) who attributed delayed germination to one or more of the following causes: (1) incomplete development of the embryo; (2) impermeability of seed testa to water; (3) mechanical restraint offered to expansion of embryo and other seed contents by the seed coats; (4) inhibition and retardation of gases to or from the embryo, resulting in accumulation of carbon dioxide within the tissues of the embryo or insufficient supply of oxygen for germination; (5) the necessity for the embryo itself to undergo certain after-ripening processes, before germination and growth under ordinary conditions become possible; (6) introduction of a condition of dormancy in seeds previously capable of immediate germination.

During the year 1934-35 the author conducted germination tests of various species of California plants. About 2000 tests, embracing some 300 species, have been made up to the time of this report, the number being sufficiently large to justify certain conclusions. The physiological and anatomical causes of delayed germination, as listed above, have been studied intensively and will be reported in another paper.

The purpose of the present paper is to discuss the germination behavior of seed of the California flora from an ecological rather than a physiological point of view. An attempt is made to determine if a relationship exists between germination behavior of the species and their systematic position, their altitudinal distribution and their habit form.

METHODS EMPLOYED

The germinating practice consisted of sowing 100 seeds in pure river sand¹ and placing the trays in a greenhouse where the temperature fluctuated between 60° and 70° F. Those seeds which failed to germinate were given different treatments such as abrasion, boiling in water, sulphuric acid bath,

¹ The writer has failed to find any advantage in using sterilized sand for germination purposes.

and finally, if all these treatments, designed to rupture the seed coat, failed to induce germination, fresh lots of the same seed were sown in moist sand and kept at 40° F. usually for a period of three months and then germinated in the greenhouse. Large seeds such as acorns, or of *Umbellularia*, *Styrax* or *Corylus* were usually germinated in peat moss.

It is hardly possible to segregate the seeds which germinate well and those which require pre-germination chilling. Many a species has seed that germinates fairly well, but chilling in many cases improves germination. This has already been shown by Nichols ('34). In the present experiments, the only species which were considered to require pre-germination chilling were those which failed completely to germinate under ordinary greenhouse conditions. Those which germinated fairly well, although benefited by chilling, were included in the group of seeds which generally germinate readily under the usual conditions.

For analytical purposes, the species studied were divided into four groups: The first represents the species whose seed germinates readily as soon as planted, and also includes plants which, although they presumably have an under-developed embryo, do not require cold temperature for its development. Such seeds usually germinated after a prolonged period under greenhouse conditions. The second group comprises plants in which delay of germination is due to the seed coat conditions such as mechanical restraint to embryo expansion, or impermeability to water and gases. The mere rupture of the teguments is sufficient to induce germination of such seeds. The third group includes those species in which germination does not take place unless the seeds are subjected to a prolonged pre-germination exposure to a low temperature; in other words, these seeds require an afterripening or so-called "stratification" treatment.² The fourth group is composed of the plants in which delay in germination is due both to impermeable seed-coat conditions and to the need for afterripening.

GERMINATION AS RELATED TO TAXONOMIC POSITION

The 300 species are distributed among 64 families. The study of the material reveals the fact that in spite of many discrepancies certain deductions can be made. The conifers germinate fairly well under ordinary greenhouse conditions, but stratification was found to be decidedly beneficial to the germination of these plants. Ordinary greenhouse germination often proceeds in such an erratic manner that it is rather difficult to ascertain the germination capacity of the species in question. Digger pine, *Pinus sabiniana*, incense cedar, *Libocedrus decurrens*, white fir, *Abies concolor*, are good examples of such behavior. The Taxaceae, represented in California by *Torreya* and *Taxus*, require a somewhat prolonged chilling of their seed before germination takes place. It is the writer's opinion that, in order to ascertain the ger-

² The term "stratification" as used in this paper presupposes presence of both low temperature and abundant moisture.

mination capacity of any California conifer, its seed should be stratified. It was found that stratification not only hastened germination of the conifers, but also "telescoped" the total germination into a shorter period of time.

Germination of gymnosperms in general is such a complicated subject that a separate paper has been prepared for publication in which this difficult problem is more fully discussed (Mirov, '36).

Among the angiosperms, the monocotyledons, with the exception of Gramineae, have not been adequately enough represented in the germination tests to permit any generalizations. In grasses, germination is easily obtained although some of them, such as *Melica torreyana*, are clearly benefited by chilling.

Among dicotyledons, the Compositae represent an outstanding example of a family in which all types, annuals, perennials and woody plants germinate well. Chilling seems to be beneficial, although not necessary, to some genera, such as *Wyethia*. The sunflower family is also exceptional in the exhibiting large percentage of sterile seeds.

Among the families whose seeds germinate well without treatment are Fagaceae, Onagraceae, Labiatae, and Scrophulariaceae.

The studies revealed that there are many plant families in which failure to germinate is due entirely to the nature of the seed coat. In such cases rupture of the testa is sufficient to promote immediate germination. The families Sterculiaceae and Anacardiaceae are good examples of this group. In the Leguminosae 16 out of 39 species examined had resistant seed coats. Of the 16 species, all save one (*Cercis occidentalis*) showed good germination when the seed coat was ruptured by the hot water treatment. *Cercis occidentalis* requires both the hot water treatment and subsequent chilling for a period of 3 months.

Stratification is essential in many families to induce germination. In the Ranunculaceae, 4 species out of 8 tested required stratification. All genera of the poppy family, with the exception of *Eschscholtzia*, required pre-germination chilling. Of the Rhamnaceae 20 species out of 32 examined did not germinate until subjected to the chilling treatment.

Species of the rose family represent a peculiar group where all sorts of influencing germination conditions are found. Some seeds, like those of *Fallugia paradoxa* or *Cercocarpus betuloides*, germinate well as soon as planted. Others, such as those of *Adenostoma*, apparently have an undeveloped embryo but do not need chilling. Still others, such as *Prunus emarginata*, definitely require prolonged chilling. There are even some, such as *Crataegus douglasii*, which require both artificial disintegration of the seed coat and also pre-germination chilling.

Many species of the rose family have one interesting peculiarity. When the freshly collected seeds are sown immediately, germination takes place readily. But when the seeds are dried and stored at a room temperature they fall into the state of secondary dormancy and should be stratified to assure

germination. Similar phenomena were noticed in cases other than the rose family, but in the latter it seems to be more common and more pronounced.

GERMINATION AND ALTITUDINAL DISTRIBUTION

For the purpose of studying the relation between the germination behavior of species and their altitudinal distribution, the experimental species were divided into three groups: low elevation, medium elevation, and high elevation plants. Table I shows the results of this arrangement.

TABLE I. *Relation of germination behavior and altitudinal distribution*

Germination behavior	Low elevation plants, 110 spp. (0-1000 feet)	Medium elevation plants, 102 spp. (1000-4000 feet)	High elevation plants, 52 spp. (4000 feet up)
Germinate readily	73.5%	69%	58%
Require afterripening at low temperatures (embryo con- dition)	10%	12%	29%
Delay in germination due to seed coat condition	14.5%	9%	2%
Delay in germination due to both seed coat and embryo condi- tions	2%	10%	11%

It is seen from table I that about three-fourths of all plants growing at low elevations germinate well. This ability to germinate consistently decreases with altitude. At medium elevations the percentage of readily germinable species is lower, amounting to 69 per cent. Among high elevation plants 58 per cent germinate readily. In other words, more than half of the high elevation species analyzed do not necessarily require low temperatures for their germination. Nichols ('34) has suggested that germination behavior connected with the effects of low temperature plays a rôle in the distribution of some species. Certainly it seems not to be the case in this group of California species. Some causes other than germination behavior determines distribution of these species.

Among the low elevation plants, 10 per cent were found to require a prolonged period of rest at low temperatures before they germinate. This is of ecological significance, since the temperatures of these altitudes are not maintained at a low enough point every year or for a sufficiently long period to promote germination of these species. This phenomenon is supplemented by the fact that in 14.5 per cent of low elevation plants germination is retarded by the hardness of the seed coat. Here again, under natural conditions, the most important factor in rupturing the testa is the variations of temperature. Of course, the rupture of the testa can also be caused by other factors such as passage through the digestive tract of birds and animals, but it appears that the influence of temperature is the one of primary importance.

To be sure, not all low elevation species are rendered germinable by the rupture of the seed coat alone. The two per cent of low elevation plants

listed in the table in which failure to germinate is due to both hardness of the testa and embryo conditions, do not tell the whole story. If we take the large genus of *Arctostaphylos* (of which only one species is included in the tabulation) we would find that all species of this genus require both seed coat rupturing and subsequent chilling for a long period of time.

A brush fire alone is not sufficient to start abundant germination of *Arctostaphylos* seeds accumulated over a period of years in the upper layers of the soil; a subsequent cold winter seems to be necessary.

It seems that hardness of the testa, which is found mostly in seeds originating at low elevations, is of considerable ecological importance. It enables the seeds to be carried in germinable condition through unfavorable periods of drought without much damage to germinability. In the majority of woody plants growing at high elevations, the hardness of the testa is associated with the necessity for a prolonged period of chilling. Rupture of the testa alone (which under natural conditions may be caused, for instance, by the passage of the seeds through the digestive tracts of animals) does not render such seeds germinable. This fact is also of ecological importance, since in the case of slowly growing woody plants, the seedlings appearing in the fall of the year would not be able to withstand severe winter temperatures. This phenomenon is pertinent to the woody plants. Low temperatures not only "stratify" the seeds but also retard germination of these plants and assure abundant appearance of seedlings in the spring when they have a better chance for survival.

GERMINATION AND THE HABIT FORM OF PLANTS

The species under consideration were divided into three groups: annuals, perennials and woody plants. The results of this arrangement are represented in table II.

Table II shows that the annuals germinate as soon as conditions of moisture-temperature are favorable. Not a single case has been detected in which California annuals require prolonged afterripening at a low temperature. Nevertheless, in many cases low temperatures help considerably as far as

TABLE II. *Germination of plants in relation to their habit form*

Germination behavior	Annuals, 36 spp.	Herbaceous perennials, 88 spp.	Woody perennials, 182 spp.
Germinate readily	91.5%	74%	52%
Require afterripening at low temperature (embryo conditions)	0%	11%	24%
Delay in germination due to seed coat condition	8.5%	15%	13%
Delay in germination due to both seed coat and embryo conditions	0%	0%	11%

better germination is concerned. This was noticed in *Festuca*, *Gilia*, *Brodiaea*, *Phacelia*, and some other plants. When delayed germination occurred in the annuals, it was due to one factor, namely the condition of the seed coat, but even so it amounts only to 8.5 per cent of the plants. In herbaceous perennial species three-fourths of all cases showed immediate germination and one-fourth gave delayed germination. This was found to be due to two causes: seed coat conditions and the need of afterripening at a low temperature. Probably seed-coat conditions are more important in herbaceous perennials than the need for chilling. In woody plants one-half of the species studied germinated well as soon as the seeds were planted, while the other half exhibited delayed germination. In this case, delayed germination might be due either to seed coat conditions or to the need for afterripening at a low temperature, or even to a combination of these two factors.

Therefore, failure of annuals to germinate was due chiefly to one cause, in perennials to two causes, and in woody plants to three causes.

SUMMARY

The germination experiments here reported appear to justify the following conclusions:

There is no consistent relation between the systematic position of a plant and its germination behavior, but certain tendencies within families are clearly indicated.

There is a definite correlation between the germination behavior of species and their altitudinal distribution. Failure of germination owing to seed coat conditions is found mostly at low elevations. Need for a prolonged period of a low temperature previous to germination, and supplemented by abundance of moisture, was found to be the most common in seeds grown at high elevations, but such conditions are necessary in many cases for seed of plants of medium and low elevations.

In the annuals, delayed germination, when it did occur, was due to one factor only, namely, seed-coat conditions. In the herbaceous perennials it was due either to a need for afterripening at low temperatures or to the seed coat conditions. Woody perennials have proven to be the most complex group. With these, delayed in germination was due to three factors: to the seed coat conditions, to the need for afterripening at low temperatures, or to a combination of both.

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THE DISTRIBUTION OF RODENTS IN OVERGRAZED AND NORMAL GRASSLANDS OF CENTRAL OKLAHOMA.

PAUL PHILLIPS

University of Oklahoma

INTRODUCTION

In the prairie region, the maintenance of conditions favorable for adequate production of grass is accomplished in nature by the development of biotic communities in equilibrium with the climate. In such communities, occasional overgrazing is perhaps common, and doubtless was present under primitive conditions, but continued overgrazing such as has been the result of poor range management by the white man has resulted in serious damage. Information necessary for correct methods of range management which will make possible permanent maintenance of favorable grassland conditions must come principally as a result of intensive range research.

Since the removal of bison, rodents and lagomorphs are the principal wild grazing mammals on ranges and often consume large quantities of forage. They are especially harmful during droughts or under conditions of overgrazing. A range may be stocked within its carrying capacity with livestock but additional pressure by rodents may result in depletion (Vorhies and Taylor, '22). Therefore, information concerning rodents and their reactions to conditions following overgrazing seems necessary for proper range management. An attempt is made to supply quantitative data regarding the relative abundance of some common rodents and lagomorphs in the various types of grassland found in central Oklahoma. The problem was suggested by Dr. A. O. Weese of the University of Oklahoma under whose guidance the work was done.

THE REGION

Data were collected in Cleveland and McClain counties, Oklahoma, from October 1, 1934 to April 15, 1935. The region in general is a rolling plain of broad, flat-topped ridges separated by wooded ravines. The underlying rocks are soft, red shales and thin, red sandstones of Permian origin. The soils are of considerable depth and moderate fertility. The region is subject to variable and extreme climatic conditions; strong dry winds, dust storms, and sudden changes in temperature are frequent. The climograph is typical of grasslands (Weese, '25). The average rainfall is 31.64 inches, the heaviest rains usually coming in May. However, downpours may occur in any month and result in considerable run-off and erosion. The average yearly mean temperature is 59.9° F. The principle growing season is the long

spring which usually is terminated by a hot dry summer. The growing season is approximately 210 days (Bruner, '31).

The true prairie, or *Stipa-Koeleria* association (Weaver and Clements, '29) extends south into this area, where little blue stem, *Andropogon scoparius*, is the dominant plant and grows in pure stands except where local unfavorable conditions resulting from erosion or heavy grazing occur. In the moister soils, *Andropogon furcatus*, *A. saccharoides*, or *Sporobolus* sp. may replace it. *Amphiachyris dracunculoides*, *Ambrosia psilostachya*, and *Draba* sp. appear as the first plant indicators of overgrazing. The later stages of depletion are indicated by *Cynodon dactylon* and *Bulbilis dactyloides*. The ravines are usually wooded, the common trees being the elm, *Ulmus americana*, the cottonwood, *Populus deltoides*, the hackberry, *Celtis occidentalis*, the persimmon, *Diospyros virginiana*, the blackhaw, *Viburnum prunifolium*, the wild plums, *Prunus angustifolia* and *P. americana*, and the red bud, *Cercis canadensis*. The buckbrush, *Symphoricarpos occidentalis*, usually occurs as underbrush.

The rodents and lagomorphs included in this study were: the prairie deer-mouse, *Peromyscus maniculatus* ssp. (probably a form intergrading between *P. m. bairdi* (Hoy and Kennicott) on the east and *P. m. nebrascensis* (Coues) on the west); the cotton rat, *Sigmodon hispidus texianus* (Audobon and Bachman); the striped ground squirrel, *Citellus tridecemlineatus texensis* (Merriam); the pocket gopher, *Geomys breviceps llanensis* Bailey, and perhaps *G. b. breviceps* Baird; the great plains jack rabbit, *Lepus californicus melanotus* (Mearns); the Oklahoma cottontail, *Sylvilagus floridanus alacer* (Bangs).

PROCEDURE AND METHODS

The grasslands were of four types: undisturbed areas, mowed hayfields, moderately overgrazed, and heavily overgrazed pastures. The first two were considered normal. Each area was classified according to the amount and kind of vegetation as determined by quadrat studies. Undisturbed grasslands supported 400 to 800 grams of little blue stem, 12 to 18 inches high, mowed hayfields supported 200 to 400 grams of little blue stem 8 to 10 inches high at the end of the growing season. Moderately overgrazed pastures supported 50 to 85 grams of little blue stem and 25 to 60 grams of weeds, and heavily overgrazed pastures supported 0 to 20 grams of little blue stem and 30 to 100 grams of weeds and sub-climax grasses. The above weights represent air-dried vegetation clipped from one square meter. Thirty separate areas averaging 20 acres each were studied, including 5 undisturbed, 10 mowed hayfields, 10 moderately overgrazed, and 5 heavily overgrazed. Areas were selected in pairs where normal and overgrazed grasslands occurred in close proximity and presented similar conditions as to exposure, topography, and surrounding vegetation. Each pair of areas is designated as a station.

For determination of the rabbit concentrations a modification of the "pellet-spot count" of Taylor ('30) was used. A wooden hoop enclosing one square foot was thrown at random 300 times in each area so as to cover it thoroughly. The relative abundance of pocket gophers was determined by counting the mounds enclosed in transects 50 feet wide extending along the traplines. The samples averaged approximately an acre per area. A similar method was used to obtain data on ground squirrels, except that the transects were only 10 feet wide, making the sample one fifth of an acre per area. The trap-night method, used by Grinnell ('14) and recommended by Taylor ('30) and Dice ('31) for estimating the relative abundance of certain small mammals was employed to obtain data on deer-mice and cotton rats. The unit is the "trap-night" which is one trap set one night. Ordinary small mouse traps were set 20 yards apart in lines, a line in normal and a line in overgrazed area, the same number of traps being effective in each type of grassland simultaneously. The same bait (rolled oats or bacon) was used in each case. The results are based on data obtained from 5010 trap nights, each station having approximately the same number of trap-nights.

RESULTS

Each animal evidently was independent in its habitat preferences. There was no apparent direct correlation between the population of any species and the amount of vegetation, with the possible exception of cotton rats. Table I

TABLE I. *Summary of rodent abundance by stations given for the general types "Normal" (N) and "Overgrazed" (O)*

Sta.	Jack rabbits pellets per sq. ft.		Cottontails pellets per sq. ft.		Pocket gophers mounds per acre		Ground squirrels dens per acre		Deer-mice per cent catch		Cotton rats per cent catch	
	N	O	N	O	N	O	N	O	N	O	N	O
1	0.25	0.47	0.18	0.21	25.60	0.00	3.50	3.50	0.00	1.14	1.14	0.00
2	0.36	0.47	0.44	0.21	0.00	0.00	8.10	0.00	4.44	2.22	1.11	0.00
3	0.40	0.46	0.72	0.18	63.50	127.10	68.50	26.30	9.74	1.95	0.00	0.00
4	0.26	0.46	0.33	0.18	37.50	127.10	36.90	26.30	0.00	2.59	0.65	0.00
5	0.19	0.33	0.30	0.25	146.51	299.87	16.10	0.00	1.11	5.55	0.00	0.00
6	0.32	0.46	0.65	0.61	147.80	49.30	21.40	0.00	0.00	3.75	20.00	0.00
7	0.05	0.23	0.06	0.20	0.00	0.00	28.60	7.20	0.00	2.50	0.00	0.00
8	0.12	0.23	0.02	0.13	0.13	13.00	0.18	0.05	1.33	6.66	0.00	0.00
9	0.17	0.17	0.14	0.09	177.90	0.00	33.30	0.00	3.57	2.86	0.00	0.00
10	0.07	0.30	0.03	0.02	15.40	94.20	61.90	42.60	0.00	8.57	0.00	0.00
11	0.21	0.72	1.66	0.62	191.20	8.18	28.50	0.00	2.00	6.00	0.00	0.00
12	0.16	0.54	0.46	0.10	43.20	0.00	0.00	4.80	2.67	2.67	0.00	0.00
13	0.59	0.85	1.31	0.41	0.00	110.11	0.00	78.65	0.00	6.67	0.95	0.00
14	0.44	0.85	1.04	0.39	0.00	23.00	0.00	12.10	1.90	2.86	0.00	0.00
15	0.59	0.43	0.49	0.12	0.00	113.74	6.05	24.10	9.52	11.43	0.95	0.00
Average	0.28	0.46	0.52	0.25	56.58	64.37	20.87	15.04	2.42	4.50	1.65	0.00

is a summary of the results obtained in each area classed as "normal" and "overgrazed." Figure 1 summarizes graphically the relative abundance of rodents in undisturbed and mowed areas, and in moderately and heavily overgrazed ranges.

Jack rabbits were found most abundant in moderately overgrazed pastures, and least abundant in mowed hayfields. The number of pellets per square foot averaged: moderately overgrazed pastures—0.51, undisturbed areas—

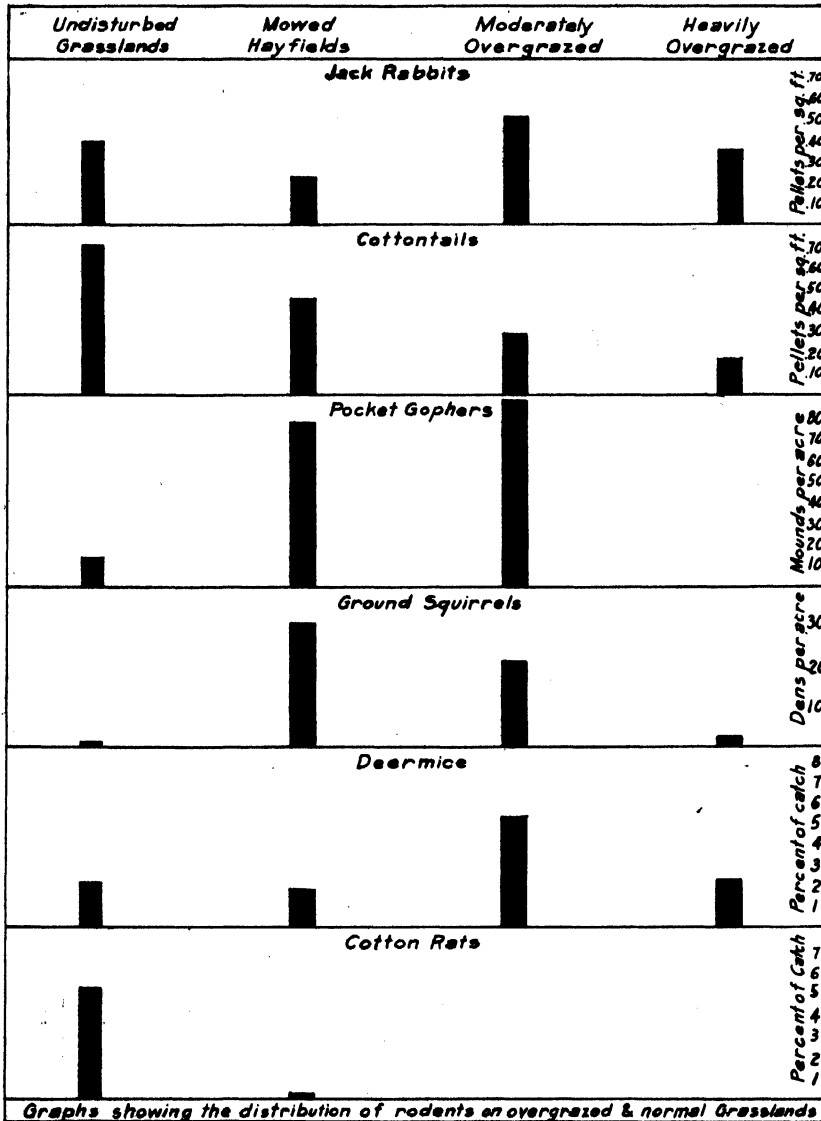


FIG. 1.

0.41, heavily overgrazed pastures—0.35, mowed hayfields—0.22, normal types—0.28, overgrazed types—0.46.

In Arizona, Vorhies and Taylor ('33) found a similar ratio between jack rabbit populations in open ranges and well grassed areas. Their results were 4.29 pellets per square foot in open ranges and 2.20 pellets per square foot

in well grassed areas. It is apparent, when these figures are compared to the present ones, that jack rabbits are about ten times as abundant in southern Arizona as they are in central Oklahoma. Previous to his work with Vorhies, Taylor ('30) made observations on the distribution of rabbits in various types of grassland but obtained opposite results. However, the later work is more conclusive and is supported by the present results and also by studies made by Taylor, Vorhies and Lister ('35), on the utilization by jack rabbits and rodents of vegetation in stock exclosures. They found that, during the winter, rodents, jack rabbits, and windfall utilized 55% of the vegetation in a cattle grazed plot to 22% in totally protected plots.

Vorhies and Taylor ('33) suggest that the distinct preference shown by jack rabbits for moderately disturbed types may be correlated with a partiality to some of the weeds and herbs of secondary successions. Evidence supporting this view was found during the present study in disturbed places where small green forbs and grasses were abundant, such as in old buffalo wallows and burned over patches. Pellets were 3 to 10 times as numerous in such places as in the surrounding grassland.

Cottontails are typically inhabitants of thickets, wooded ravines, weedy places, and other types with abundant cover. This characteristic preference is apparent in the results of this investigation. Pellets were most abundant in undisturbed grasslands, and were least numerous in heavily overgrazed pastures. The number of pellets per square foot averaged: undisturbed areas—0.70, mowed hayfields—0.44, moderately overgrazed pastures—0.28, heavily overgrazed pastures—0.18, normal types—0.52, overgrazed types—0.25.

Where small patches of short green forbs occurred surrounded by well grassed areas, the pellets were especially abundant, indicating that cover plus food makes an area especially attractive to these animals. These results differ from those of Taylor ('30) who found that, in Arizona, cottontails prefer the open, semi-desert types.

Pocket gophers were definitely more abundant in mowed hayfields and moderately overgrazed pastures than in undisturbed areas and were entirely absent in heavily overgrazed pastures. The number of mounds per acre averaged: moderately overgrazed pastures—87.78, mowed hayfields—77.89, undisturbed areas—13.80, heavily overgrazed pastures—0.00, normal types—56.58, overgrazed types—64.37.

They seemed to prefer the varied vegetation of disturbed grasslands and were most abundant in these types providing the soil was favorable for burrowing. This preference was clearly apparent in moderately overgrazed areas where forbs were present in scattered, well-defined patches, separated by pure stands of short little blue stem. The gopher mounds were distributed in groups approximately coincident with the patches of forbs.

It is possible that the greater imperviousness of soils in heavily overgrazed areas is both cause and result of the absence of pocket gophers. Formosov ('28) states that burrowing rodents in the steppes of Russia rework the soil

to such an extent that the vegetation is kept in sub-climax condition which is more favorable for them. The action of the rodents on the soil opposes that of hoofed animals and an equilibrium is maintained inside the associations of the steppes. Similarly, pocket gophers occupy an important niche in the prairie association of this country and according to Grinnell ('23) should not be eliminated from grazing lands because they counteract the packing effect of hoofed animals.

Ground squirrels were most abundant in mowed hayfields. The number of dens per acre averaged: mowed hayfields—30.3, moderately overgrazed pastures—21.5, heavily overgrazed pastures—2.4, undisturbed areas—1.9, normal types—20.87, overgrazed types—15.04.

Apparently, drainage is an important factor in the distribution of this animal as dens are restricted to well drained soil. In one area, burrows were confined to small dry knolls surrounded by moister lower soil. Bailey ('26) gives open grassy ridges and dry prairies as favorite habitats in North Dakota, and Wood ('10) says they are most numerous on prairie hills in Illinois. The data obtained in connection with this study do not seem to agree with the statement made by Weaver and Flory ('34) that overgrazing always results in an increase in the striped ground squirrel population.

Deer-mice reached maximum abundance in moderately overgrazed pastures. The percentages of catch were: moderately overgrazed pastures—5.32, heavily overgrazed pastures—2.38, undisturbed areas—2.31, mowed hayfields—1.97, normal types—2.42, overgrazed types—4.50.

Deer-mice were abundant in a mowed field which was rather badly eroded and had a foliage cover of less than 50 per cent. In only two instances were they taken in appreciable numbers in high grass types; in the first, all of them were caught in a small burned area; and in the second, the entire area previously had been burned, and although the grass was tall there was a large proportion of bare area. These results support the opinion of Johnson ('26) that the deer-mouse "must have belonged to some sub-climax communities rather than to the *Andropogon* climax type of prairie association." Cogshall ('28) lists ragweed and dandelion seeds as important foods of the deer-mouse. Both plants are sub-climax forms on the prairie and often are found in overgrazed areas. They probably constitute a factor affecting the habitat preferences of this animal.

Cotton rats were almost wholly restricted to the abundant cover of undisturbed grassland. The percentages obtained were: undisturbed areas—5.10, mowed hayfields—0.20, moderately overgrazed—0.00, heavily overgrazed—0.00, normal types—1.65, overgrazed types—0.00.

This animal makes runs and rarely is taken outside them. Many individuals were taken during the diurnal period of the day. Strecker ('29) remarks that they feed largely at this time. In heavy grass growing in moist soil catches were especially high.

SUMMARY

Comparative data were obtained on the distribution of various common rodents and lagomorphs in grasslands of central Oklahoma. Pellet counts indicated that jack rabbits were most abundant in moderately overgrazed areas and cottontails preferred the cover afforded by undisturbed grasslands. Mound counts showed pocket gophers more numerous in mowed hayfields and moderately overgrazed pastures than in either heavily overgrazed or undisturbed areas. Ground squirrels occurred more often in mowed hayfields. Trapping showed that deer-mice were most numerous in moderately overgrazed grassland while cotton rats were almost entirely restricted to heavily grassed undisturbed areas.

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REVIEWS

QUAIL POPULATION STUDIES IN IOWA AND WISCONSIN ¹

Errington's studies of quail populations, appearing in various journals since 1930, have probably been something less than clear to some readers. The first thing to be said for the present bulletin is that it dissolves most, if not all, of the ambiguity which limitations of space and continuity imposed on his less comprehensive publications.

Stoddard's "Bobwhite," based largely on studies in Georgia, has been generally accepted as the most successful attempt to explain in ecological terms what determines the population level of an American upland game bird. This bulletin easily takes rank as the second. In fact, the superior censusing facilities offered by northern snows makes this, from the viewpoint of population measurement, perhaps a more satisfactory work than Stoddard's.

The bulletin presents winter survival data on more than 11,000 quail in about 800 coveys followed through six winters in Iowa and Wisconsin. The field methods by which the census and mortality data were obtained are for the first time described and explained in detail. It was, of course, impossible to do this in each of the shorter papers. This may be one of the reasons why the present bulletin is more convincing than its predecessors. To reduce to paper and ink the woodsman's skill in "reading sign" used by Errington and his assistants is perhaps not the least of his contributions to science, especially in an age when this skill has been atrophied in most laboratory workers.

What happened to the 11,000 quail? Our authors interpret their survival data in terms of this hypothesis: There exists for each unit of territory a norm or limit of population density which its food and cover combinations are capable of supporting through a normal winter. Interplaying with this external inhibitory force is an internal intolerance of concentration, tending, by current movements of coveys or individuals, to adjust population to carrying capacity. The net resultant is a tendency for each unit to emerge from the normal winter with not more than so many birds, regardless of (1) how many it had in fall, (2) what kind or how many predators operated on them.

In other words, population fluctuates about a norm by reason of superior survival or reproduction below it, and accelerated mortality above it. The surplus, or population above carrying capacity, seems to be vulnerable, *i.e.*, it either leaves, starves, freezes, or gets caught, but the secure population below suffers only nominal mortality, except in years of exceptional snows.

¹ Paul L. Errington and F. N. Hamerstrom, Jr. 1936. The northern bobwhite's winter territory. *Iowa State College of Agriculture, Research Bull.* 201.

or other emergencies. When reduced below capacity, population quickly rebounds to normal.

The authors do not purport to understand just how carrying capacity limits survival with such apparent exactness for successive years. They do, however, believe that their data support the hypothesis, and that, while it applies most clearly to larger units of territory, it also holds good for surprisingly small units, even some single covey ranges.

Can the critical reader agree with these conclusions? This vital question is conditioned, first of all, by certain adjustments and selections of data made to segregate abnormalities. These are made partly on a basis of personal judgment, but the data seem to support the hypothesis fairly well without them. Especially reassuring is the simple fact that variations in mortality exist as between a series of adjacent territories and these variations, by persisting through a series of winters, indicate that each expresses a characteristic of the territory as related to the bird. This characteristic is called carrying capacity.

Some critics will doubtless question the hypothesis on the ground that the data are observational, and the conclusions unchecked by controlled experiments. Undoubtedly the investigators should next attempt to raise the carrying capacity of more of their sample areas by food and cover manipulation, and then see what happens. But to "see what happens" is again observational science. We are confronted, in short, by the obstinate fact that the wild relationships of wild populations are in general *not susceptible* to controls in the laboratory sense. Moreover, a certain amount of fortuitous manipulation has already occurred through changes in farm practice, CWA debrushing, and other disturbances. These, as the authors point out, have been as good, and cheaper, than deliberate manipulations of carrying capacity by the investigators.

The deductions from this study may be tentative, but the fact that it breaks new scientific ground is hardly open to debate. Nor is there any doubt that other countries have felt the identical and simultaneous impulse to explore the same general subject. Elton and Middleton in England, Vietinghoff in Germany, Nicholson in Australia, Severtzoff in Russia are among those seeking to unravel population behavior in the birds and mammals. There is, of course, a larger number working with lower organisms subject to laboratory experimentation, and their work is further advanced. Some day the two fields must be related to each other. It is such work as the present bulletin which will enable this to be done.

The Errington papers have always been conscientiously constructed, but the present work shows evidences of a developing clarity, simplicity, and grace not found in the earlier publications of either author.

ALDO LEOPOLD

UNIVERSITY OF WISCONSIN,
MADISON, WISCONSIN

A PERMANENT SYSTEM OF FLOOD CONTROL ¹

A hearing on the following bill was held before the H. R. Committee on Flood Control on May 21, 1936, in Washington, D. C.:

"Be it enacted by the Senate and House of Representatives of America in Congress assembled, That for the purpose of establishing a definite and permanent system and policy of flood control and for the acquisition of forest lands on which the restoration and maintenance of suitable forest conditions will aid in preventing and controlling floods at their source, under the provisions of the Act approved March 1, 1911 (36 Stat. 961; U. S. C., title 16, secs. 500, 513, 515, 516, 517, 518, 519, 521, 552, and 563), as amended, and of the Act approved August 29, 1935 (Public, Numbered 395, Seventy-fourth Congress; U. S. C., Supp. 1, title 16, secs. 567a, 567b, and 567c), and for necessary expenses incident to conducting on lands acquired under the aforesaid Act of March 1, 1911, as amended, such reforestation, and other protection, improvement, and development work as may be required, for the determination of form and conditions when forests will render the most effective watershed services, and for cooperative protection improvements and facilities on watersheds pursuant to sections 1 and 2 of the Act approved June 7, 1924 (U. S. C., title 16, secs. 564 and 565), as a further aid in preventing and controlling floods, there is hereby authorized to be appropriated the sum of \$250,000,000."

The bill was introduced by Rep. C. V. Parsons of Illinois on April 29, 1935, following the unusually heavy spring floods in the eastern part of the country. The technical aspects of the need for a permanent system and policy of flood control were given by L. F. Kneipp of the forest service.

An interesting feature of the hearing was the discussion, by various representatives, of the question of increasing occurrence and severity of floods following the clearing and cultivation of hill lands in eastern United States during the past 30 to 80 years. It was brought out that large floods occurred in the past, before there was a great deal of watershed devastation in the east, under peculiar climatic conditions, and that such conditions would doubtlessly obtain again; however, because of forest denudation and improvements associated with an increasing population a greater number of floods have occurred in the recent past and the damage from them is greater than before. In other words, because of a greater and more rapid run-off, the amount and duration of precipitation necessary for flood conditions of major importance is less now than before extensive removal of watershed forests, and as a result many more destructive floods occur.

The work of the W. P. A. and the C. C. C. on erosion control and watershed protection appeared to have confused the need for the proposed legislation. However, it was pointed out that one of the main features of the bill

¹ Committee on Flood Control, House of Representatives, Washington, D. C., 1936. Hearing before the Committee on Flood Control, House of Representatives, Seventy-fourth Congress, Second Session on H. R. 12517. To provide for a permanent system of flood control, and for other purposes. May 21, 1936.

was to authorize purchase of pertinent lands that could not, apparently, be obtained through regular channels.

The necessity of controlling waters at their source was aptly expressed by one individual who pointed to the vast sums that have been expended for flood control in the lower Mississippi valley as compared to those expended on upper tributary streams and their watersheds.

The Forest Service presented data and observations, in support of the bill, obtained largely from the Copeland Report "A National Plan for American Forestry." An informative table was presented giving data on forest-land acquisition under the Weeks and Clark-McNary laws by land exchange and by withdrawal from the public domain, and the current land and financial status of established purchase units as of April 3, 1936.

The need for a long-range plan in which engineering works on rivers and reforestation of watersheds are properly weighted as to their individual and combined value for flood control was indicated.

T. S. COILE

DEPARTMENT OF FORESTRY,
DUKE UNIVERSITY

THE GREAT AMERICAN SHELTER-BELT ¹

Newcomer to the traditional bed of politics, ecology is not therefore to be judged a mere transient. The entire problem of modern civilization is emerging into its true light, as a vast, ecologically conditioned enterprise. It is essential under the circumstances that the ecologist distinguish clearly between his function as an adviser in determining broad policy and his task when called upon to execute any policy, once it is promulgated. So far as the record before us is concerned, the Forest Service has acted in the latter rôle with respect to the Great American Shelter-Belt. What part if any its individual members may have played in launching and finally throttling the enterprise is a question for the historian of politics. To the reviewer the report cited above is a competent technical document, executed by a staff intent upon the proper discharge of a difficult assignment.

The first chapter prepared by Zon epitomizes the results of preliminary study upon the procedure to be adopted, including even the difficult economic aspects. The second applies these studies to a forecast of probable effects. Both chapters are decidedly in harmony with the general realism of the whole report. The reader who searches for picturesque and extravagant claims will be disappointed.

At the start it is emphasized that shelter-belt planting can only represent one aspect of a comprehensive land management policy, and that its benefits must come from local amelioration rather than any influence on climate as

¹ Zon, R. 1935. What the study discloses. (in) *Possibilities of shelterbelt planting in the plains region*. Sec. 2: 3-10. Washington.

———. Prospective effects of the tree-planting program. *Ibid.* Sec. 6: 33-38.

such. Roughly following the 99th meridian from north to south, the area selected lies on the tension zone between prairie and short-grass—manifestly not in a forest climate. Survey and experiment indicate however that nearly 60 per cent of this 100-mile wide zone lends itself to tree planting, properly supervised. No Chinese wall of forest, but a combination of field-plantings, wind-breaks, and some block-planting is recommended, all with due regard to soil, topography and water supply. Close spacing, diversity of composition, and a stream-line top contour are recommended. The necessity for especial care and expense are conceded, as well as the need for continued research. With regard to the effects of wind-breaks upon adjacent land, for example, there can be no brief and generally true answer for such a diverse region.

Personally, the reviewer regards the work already done by the Forest Service on this plan as a remarkable example of applied ecology. Those who are inclined to criticize its participation as an unbalanced emphasis on one aspect of a huge problem of restoration must remember that it is not, primarily, an agency for the determination of policy.

The Great Shelter-Belt project clearly exemplifies the strength and weakness of our modern technological culture. Whenever a specific enterprise is determined upon, the most remarkable facilities are at hand to insure its effective execution. In this lies our strength. But when we face the deeper question of the plan behind all plans, our weakness is revealed. In that matter we seem to have no technique that was not known—and tried—in the ancient world. The modern administrator has at his disposal infinitely better technical facilities than had Augustus or Alexander, and a correspondingly greater obligation to know just what he is about. But the advance of human knowledge has provided no new way to relieve him of the lonely task of decision.

One conclusion however seems clear enough, now that the Congress has dried up the financial source which fed the Shelter-Belt during its brief and meteoric course. Had it been possible to assign the whole problem of land utilization in the grassland area to some group as capable, experienced and as closely integrated as the Forest Service, a valuable plan might have been developed. What the exigencies of politics would have done with it is, of course, another matter.

PAUL B. SEARS

THE UNIVERSITY OF OKLAHOMA,
NORMAN, OKLAHOMA

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NOTES AND COMMENT

THE COMING ECOLOGIST

The determination of the relation of living organisms to their environment constitutes the main aim and purpose of ecology. While the experimental determination of the various factors which enter into this complex problem is essential, it should be preceded and accompanied by general field observational work. The latter is necessary not only in order that the experimental work may be well-balanced in relation to the broader aspects of the ecological field, but it should provide the bond by which the results obtained from more intensive study may be coordinated and united.

Because of its breadth of interest, involving as it does practically all the sciences in their relation to the living world, ecology, at least in its more general aspects, should have an important place in general education. Its broader outdoor phases have an inspirational value which is often lacking in more concentrated (especially indoor) work; its many-sided interests and relationships make it an admirable introduction to all sciences, in fact approaching an ideal "general science," limited neither to the biological nor physical sciences, nor consisting of a disconnected smattering of all of them; and it should perform a much needed service in counteracting the narrowing influences of extreme specialization.

Perhaps before these general cultural possibilities are fully realized, it will be necessary for ecologists themselves to recognize and proclaim them.

On the side of pure science, ecology offers innumerable attractive problems, to the solution of which every science must contribute. This very circumstance, however, very often results in disconnected series of investigations which resemble a pavement with irregular unfinished gaps along its entire course.

A vast amount of research is still necessary, but in the main this should be correlated and coordinated under a general plan or effort embodying the full recognition of *all* physiological and environmental influences upon the individual and communal life and behavior of organisms.

It is self-evident, and is being more and more clearly recognized in practice, that no one worker can compass the entire field, for neither the span of a single lifetime, nor the capacity or training of any single mind, can make this possible. It is therefore necessary that closer cooperation be established between individuals, departments and regional groups.

This is often difficult because of the fears or jealousies of individuals and the exclusiveness of departments and special groups, and perhaps the difficulty is increased by the not uncommon tendency to establish ecology as a distinct science apart from others instead of a common bond between all of them. A cooperative effort, similar to that made a few years ago in the field of absorption, is highly desirable.

The very breadth of the ecological field and the complexity of its problems, give little hope that the necessary many-sided basic information can be secured by scattered individuals working independently in limited segments of the great field.

All who have had experience in the field in observational and experimental work know the difficulties which arise if excessive segregation is attempted. In the field it is impossible to limit attention to a single object or condition. Such segregation is often possible in the laboratory by the control of various factors, but in the natural world all the interrelated factors are more or less in operation at the same time, and the omission or faulty interpretation of any one of them may be fatal to the conclusions reached.

The various factors, moreover, are not constant in their influence. They may be absent, or vary in degree in different environment; and they are sure to vary in intensity and effect in the same locality, each being at times positive, negative or neutral, and this often independently of the others. The difficulties are further increased by the fact that these factors fall within the scope of different departments of science and cannot be approached with equal assurance and judgment by any one individual.

Since each of these factors, therefore, may actively counteract or reinforce the effect of the others, they cannot be considered separately and at different times, but must be determined simultaneously. They should also be continued at the same point for long periods, often beyond the lifetime of any individual—especially where they are related to variable climatic influences.

All this is manifestly impossible for individuals or very small isolated groups, but calls for broad cooperative work.

Perhaps the hope of complete cooperation in this work is a Utopian dream, but it should be the chief function of an organization such as ours to work towards its realization.

This is now being done to some extent, but the effort should be increased. Perhaps the plans now being made and in part carried out, to establish study centers in suitable regions, may bring us nearer to a realization of this dream, but above all it is essential that this cooperative effort be not confined to committees or limited groups, but that all ecologists become conscious of its need and carry on their work in its spirit.

Perhaps a long step would be taken in the desired direction if we recognized more completely (in practice) the unity of so-called plant and animal ecology. There will, of course, always be individual workers who will place greater emphasis on one group of organisms than the other, and there will be problems which are related more particularly to either plants or animals alone, but on the whole they are so interrelated that they blend into an indivisible whole.

This points to the need of the development of another phase of ecological work. We have placed emphasis on the experimental determination of the physical factors, and no one will question the need and the value of such work. But exact quantitative results are of value *only* for comparative purposes, for the combination of factors is never exactly the same at any two periods. They should therefore be made simultaneously at the various stations which may be established (and these should be numerous, in divers locations); they should be continued for long periods; and they should be made not once, or even two or three times a day, but at least every hour, where self-recording apparatus is not available, in order that the effect of the divers fluctuating characters may be noted.

But this determination of physical factors is not sufficient. We have much to learn concerning the relative ecological influence of the members of our biota, particularly upon competition and shelter and upon the supply of food and oxygen. The investigation of these mutual biotic ecological reactions should also be both experimental and observational, and it should be broad enough to cover ultimately all the influences, good and evil, exerted by each member in that endless chain (or more properly maze) of ecological relationships displayed in the living world, in order that the net influence of each may be determined accurately for each regional type.

Here, again, cooperation, especially between botanists and zoologists, is essential.

It is true that some progress has been made in this direction, but how much is still lacking is revealed whenever a new research problem is approached, or an effort is made to develop some of man's many interests which require basic ecological knowledge.

The importance of the latter is becoming more and more evident. Recently Clements (*Ecology* 16: 342-363) has emphasized the application of ecological principles to such practical problems as land classification and uses, forestry, grazing, shelter-belts and landscaping.

That these are primarily ecological problems is obvious, but the field should be extended. When we drain and irrigate, clear forests and conserve soils, protect wild life and preserve natural areas, perpetuate our forests, prevent the pollution of our waters and guard against floods, we are simply trying to make it possible to grow something for man's use, and all these problems are basically ecological. Yet in nearly all cases the ecologist is almost entirely ignored, and his functions are assigned to or assumed by the engineer, the meteorologist, the landscape artist and the practical forester, or the narrow specialist who works out minute details in his own particular field, but overlooks or disregards considerations which do not lie within his own narrow perspective.

The ecologist should provide the basic facts and principles upon which all these applications to man's interests are (or should be) founded, and these must be based not only on the quantitative determinations of physical factors and the distribution or relative location of members of the biota, but also on an understanding of the mutual ecological relationships existing between the latter.

He should be the consultant in all conservation problems. There has been a disposition on the part of certain interests to usurp the term "conservation" for merely its recreational features, and, unfortunately, some ecologists passively accept this. In truth, conservation properly compasses all the problems which arise from any tendency towards changes in natural conditions, whether they result from natural causes or are induced artificially by man's interference in his efforts to advance his own interests. It therefore distinctly includes the practical problems which have been noted, and which are basically ecological.

For several reasons the ecologist should not scorn even the recreational features of conservation. Recreational parks, state and national, and fish and game preserves, as well as bird sanctuaries, are receiving much public support and attention. Their problems are also essentially ecological, and, moreover, they offer possibilities of the preservation of natural areas which should not be overlooked. The ecologist should give particular attention to them because there is danger that those who are not ecologically-minded will secure control of the areas best suited to his researches, and will ruin them for his purposes.

It will do but little good to stand aloof and protest. We can accomplish much more by making it clear that ecological considerations are all-important even to the recreational phases of conservation, and then tendering our services to their proper advancement. Such services, based on a wider understanding of the ecological problems involved, should replace many of the "research" studies now being made on narrow detached problems, which cannot be solved separately, or the bungling efforts of those who lack ecological training.

We will then, also, be in a position to ask that in the larger national and state parks distinct natural preserves be set aside for research purposes.

In thus turning his attention to practical problems of public interest the ecologist should not commercialize his field, nor would it be particularly desirable to emulate some of our sister sciences and set up the profession of "ecological engineer," with the probable consequent slighting of the basic science. He should, however, particularly develop those phases of his work which will be of value in public service, and make their importance known.

The coming ecologist must be a broad-minded student of his scientific problems, imbued with a spirit of cooperation, and willing to give the best at his command to public service.

B. SHIMEK

DEPARTMENT OF BOTANY,
STATE UNIVERSITY OF IOWA.

THE EFFECTS OF CONTINUED EXPOSURE TO MOISTURE ON THE
WEIGHTS OF FERTILE AND NON-FERTILE EGGS OF THE
SLUG, *LIMAX FLAVUS* L.

EMMETT B. CARMICHAEL

University of Alabama

Eggs of the slug, *Limax flavus* Linnaeus, lost weight very rapidly when placed on dry filter paper (Carmichael and Rivers, '32). The eggs were covered with a membrane which allowed this exchange of moisture. Since this membrane was not rigid it was decided to determine whether the weights of the eggs would remain the same until the time of hatching if they were allowed to be in contact with moist filter paper. Hayes ('30) found that the wet weight of salmon eggs increases slowly until a short time before hatching and then rapidly.

The slug eggs were laid in the laboratory. After being separated and washed, they were placed on moist filter paper until they regained any weight which they had lost either during the time required for laying or in the case of those that were laid during the night, until they were observed the next day. Tap water was used for washing and for moistening the filter paper. The different batches of eggs were left on the moist filter paper for varied lengths of time previous to the first weighing, but the periods were always of several hours duration. The eggs, when laid, were fastened together by a connecting membrane and thus necessitated being separated before starting the experiment. After a few hours of preliminary moistening, the eggs were placed on dry filter paper for about thirty seconds in order to remove the external moisture. The eggs were weighed and placed back on moist filter paper. The above process of weighing was repeated at intervals of a day or more up to the time of hatching. Non-fertile eggs, as controls, were carried through the above procedures.

Figure 1 illustrates the effects on the weights of fertile and non-fertile slug eggs which have remained in contact with moist filter paper. The data are averages of the weights of the eggs in whole batches and a single curve represents effects on one batch.

The curves in figure 1 are given as representative ones of the several batches which have been observed. Several of the curves are somewhat irregular during the first few days of the experiment. There was a marked increase in the weight of the fertile eggs after about the eighth day, figure 1, A. This increase was accelerated until the eggs reached a maximum weight which occurred in most cases between the fifteenth and eighteenth days after being laid. Then there was usually a rapid loss in weight until the hatching began. When a majority of the eggs in a batch had hatched, the weighings were discontinued. As controls, non-fertile eggs were allowed to remain on moist filter paper for definite periods which correspond to the time required for hatching of fertile eggs, figure 1, B.

The increases in the weights of the non-fertile eggs in 15 to 18 days were never as great as they were in the case of the fertile eggs. That the weights of most of the batches of control eggs given here are not the maximum weights that could have been attained is fairly certain since a majority of the curves show that the eggs were increasing in weight at the time these particular experiments were discontinued.

DISCUSSION

At first it was expected that the fertile eggs would suffer a gradual loss in weight until the young embryos were almost mature and then a more rapid decline was anticipated. Most of the curves are somewhat irregular for the first few days. This fact is partially explained because of the connecting tissue that remained on the ends of the eggs

when the experiments were started. This material was gradually lost during the course of the experiment. Regardless of this irregularity of the curves during the first few days, the fertile eggs increased in weight up to a rather constant period and then lost weight rapidly for a few days. In the case of the fertile eggs this loss in weight was in-

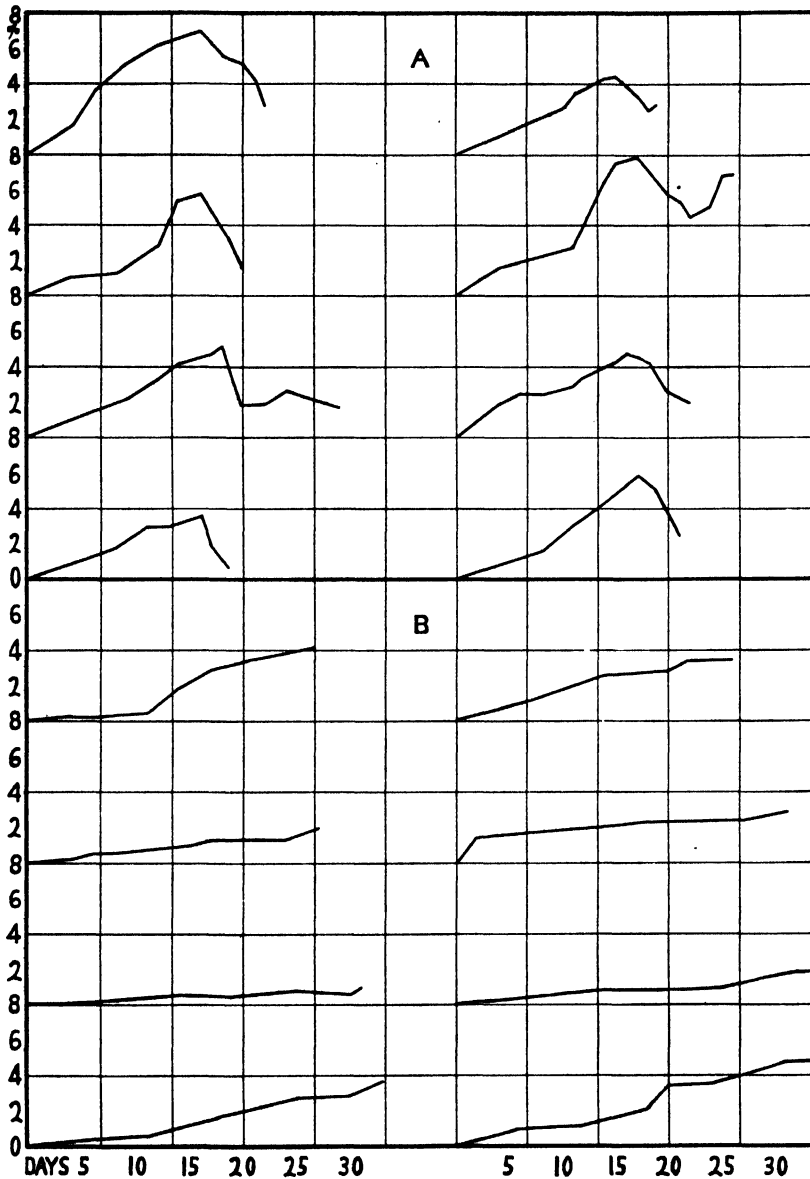


FIG. 1. The per cent increase in weight of slug eggs that have been allowed to be in contact with water: A, fertile eggs, and B, non-fertile eggs.

terruted by some of the eggs hatching. The loss, however, was never great enough to bring the eggs to the weight which they had at the time the experiment started. Non-fertile eggs, which served as controls, always increased in weight and this increase varied considerably between the different batches. There was no indication of a decrease in weight of these eggs as there was in the case of the fertile eggs.

The decrease in weight of the fertile eggs was very probably due to the loss of metabolic products and this subject is being studied.

SUMMARY

1. The maximum increase in the weights of fertile slug eggs varied from about 3.5 to 7.9 per cent. This maximum weight was usually attained about fifteen to eighteen days after the eggs were laid.
2. There is a rather sharp decline in weight of the fertile eggs after the maximum weight is attained.
3. Hatching begins before the eggs drop to the weights which they had had at the beginning of the experiments.
4. Non-fertile eggs increase in weight and they do not show a decrease in weight even if carried over a much longer period than normally required for the hatching of normal young slugs.
5. The increase in weight of the fertile eggs is much more pronounced than it is in the case of the non-fertile eggs.

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SELECTIVE HABITAT OF THE POISONOUS *ASTRAGALUS HYLOPHILUS*¹ (RYDG.) A. NELS.

The toxicity of certain Astragali of the Rocky Mountain region is a matter of major economic importance among stockmen. Those of significance as livestock hazards have been referred to by several investigators. The increased activation caused by the toxic element selenium was first reported by Beath² and co-authors in 1934. The distribution and toxicity of those Astragali that absorb toxic quantities of selenium is an interesting and unexplained development. This group at the present time includes the following species: *A. racemosus*, *A. bisulcatus*, *A. scobinatulus*, *A. grayi*, *A. flaviflorus*, *A. pectinatus* and *A. haydenianus*. Of these, *A. grayi* is the only one that appears to be confined exclusively to soils and shales of Cretaceous and Eocene origin. The others occur frequently upon soils of a non-seleniferous nature and consequently under these conditions are free of selenium. Occurring on seleniferous shales and soils they become heavy absorbers of selenium. From outward appearances there is nothing to indicate whether or not selenium is present. Certain ones, particularly *A. racemosus*, *A. bisulcatus*, *A. scobinatulus* and *A. haydenianus* develop a very obnoxious odor if the element selenium is present.

Astragalus hylophilus is a particularly troublesome poisonous plant to livestock men in south-central and southwestern Wyoming. Time and space will not be taken here to point out these characteristics. Wyoming Station Bulletin 189 on "Three Poisonous Vetches" may be consulted for these details. Unlike the Astragali referred to above, selenium is not a factor in activating the toxic principle or principles in *A. hylophilus*. The pathology of diseased animals points definitely to toxic mineral activation. Tin,

¹ *A. campestris* Gray (*A. hylophilus* (Rydg.) A. Nels.), *Homalobus hylophilus* Rydg.

² Beath, O. A., et al. 1934. Certain poisonous plants of Wyoming activated by selenium and their association with respect to soil types. *Jour. Am. Pharm. Assn.* 23: p. 94.

molybdenum and arsenic in organic combination have been isolated from plant extracts. The restrictive growth of *A. hylophilus* on definite geological formations is a matter of ecological importance. In Wyoming it has not been found to occur on any other soils than those derived from the Hanna and Bishop conglomerates. Transplanting young, thrifty plants to soils common to mountainous areas other than the two geological formations mentioned above has, as yet, not been successfully done.

Definite proof of the restricted habitat of *A. hylophilus* was further determined during the past season. In Deep Creek canyon in the old Hayden National Forest (now Medicine Bow) of south-central Wyoming there occurs a series of well exposed geological formations. From the forest boundary to the edge of the canyon travelling south one is on the Hanna conglomerate. At the point where the road starts to descend the canyon, older sediments are noted in regular sequence from the Frontier to the Chugwater. The demarcation of *A. hylophilus* in this area is critically exacting. It could not be found to occur even in scattered patches on any geological formation except the Hanna conglomerate.

Another area was selected in southwestern Wyoming in Uinta County near Lonetree for further critical study of *A. hylophilus* distribution. In the valley floor of this region the type geological formation is the Bridger (Eocene). As one traverses toward the foothills to the west the Bridger terminates and the Bishop conglomerate then becomes the dominant geological formation. This continues until one approaches the quartzitic core of the Uinta mountains. *A. hylophilus* here is confined exclusively to the Bishop conglomerate. It was not possible to find any plant growth of *A. hylophilus* on the Bridger, although other *Astragali* were observed. The fact that the growth of *A. hylophilus* is confined to definite geological formations means that the plant's existence depends upon certain soil constituents held by these particular conglomerates. The Hanna and Bishop conglomerates according to Dr. S. H. Knight, Professor of Geology and State Geologist of Wyoming, have the following history:

"*The Hanna formation.*—In its type locality the Hanna formation is composed of a thick succession of sandstones, shales and coal seams. The formation thins rapidly and exhibits a marked change in its character as it is traced from its type locality in the Hanna Basin toward the flanking mountains. The sandstones and shales merge laterally into beds of arkose grit and conglomerate. The formation rests upon the upturned and eroded edges of all the older rocks including the ancient pre-Cambrian crystalline and metamorphic rocks. The physical character and position of this formation in the rock column demonstrates conclusively that it is made up of rock debris which was eroded from all the older rocks in the local geological column. Fragments of the more resistant beds of pre-Cambrian, Paleozoic and Mesozoic age are readily recognized in the conglomeratic phase of the formation. The rock debris was deposited on the flood plains of rivers which drained from the mountains into the adjacent basins. Outcrops of the formation are conspicuous along the eastern flank of the Medicine Bow Mountains and throughout the Pass Creek, Carbon and Hanna Basin which lie north of the Medicine Bow Mountains. Rocks believed to be of Hanna age cover a considerable area along the west flank of the Sierra Madre or Encampment Mountains. The Hanna formation has been correlated with the Fort Union formation which is Paleocene in age.

"*The Bishop conglomerate.*—This formation consists of boulders and pebbles embedded in a finer matrix of gravel and sand. The formation has a maximum thickness of 200 feet. It occurs in large isolated patches which cap upland ridges and peaks in Uinta and Sweetwater counties, Wyoming. Occurrences are also found high on the south flank of the Uinta Mountains in Uinta and Duchesne Counties, Utah. The physical character of the rock debris which makes up the formation shows that it was derived from the Uinta Mountains. It is concluded that the formation was deposited by rivers which flowed over a remarkably even surface which truncated the structure of the older rocks and which sloped away from the mountains. The exact age of the Bishop conglomerate is still in question. It is known to be younger than Eocene. It may be of late Oligocene or lower Miocene age."

Astragalus hylophilus referred to by some investigators as the "timber milk vetch" has in addition to its selective soil preference another unique habitat in that its occurrence

in areas within the Hanna and Bishop conglomerates is quite generally confined to aspen growths, aspen-pine associations and pines. Under suitable soil and moisture conditions the continuity of growth is so persistent that the ground frequently is more or less completely covered by it.

The destructive character of *A. hylophilus* upon cattle and sheep has at intervals reached alarming proportions. Its confinement to the soil types and shaded areas mentioned by the author should make it possible for grazing interests to institute measures of precaution and control that would in some measure offset the present policy of aloofness and chance-taking. Possibly further research will show that this vetch in certain areas is more potent than in others. It is not known at the present time whether such a variation occurs or not. Corresponding evidence is available for those *Astragali* that absorb selenium. It has been definitely established that there are areas within areas that are particularly poisonous largely because of the greater absorption of selenium. If it should develop that the same principles of activation would apply to *A. hylophilus*, then measures of control would be much easier to carry out.

The "timber milk vetch" may, therefore, be taken as an indicator plant of the geological formations *in situ*, viz., the Hanna and Bishop conglomerates. It occurs widely distributed on these formations but within the restrictions referred to above.

O. A. BEATH

UNIVERSITY OF WYOMING,
LARAMIE, WYOMING

THE EFFECT OF SOIL TYPES ON THE HELMINTHS PARASITIC IN THE GROUND LIZARD, *LEIOLOPISMA LATERALE* (SAY)¹

PAUL D. HARWOOD

Zoological Division, U. S. Bureau of Animal Industry, Washington, D. C.

INTRODUCTION

The data upon which this paper is based are all derived from collections and observations made within 20 or 30 miles of Houston, Texas. The land in this region is all very flat and, therefore, any possibility of changes in the fauna due to altitude may be disregarded. The small extent of the area excludes differences due to latitude as a factor. The data herein presented are admittedly too few to permit the drawing of any detailed conclusions, but as there will not be an opportunity in the future for extending the observations it is thought best to report them at this time. I am greatly indebted to Dr. A. C. Chandler for advice in the preparation of this paper.

Description of soil types and parasitic fauna of hosts found on these soils

The host animals, *Leiopismania laterale* (Say), have been collected from certain limited areas, each area known to consist of a single soil type. The types of the soils were determined by consulting the *Soil Survey of Harris County, Texas* (Geib, Bushnell and Bauer, '22) and the *Soils of Texas* (Carter, '31). The lizards were all examined within a day or two of capture, and the number infested recorded. Only such parasites as are very common in *Leiopismania laterale* about Houston were considered. These include *Brachycoelium daviesi* Harwood, *Cylindrotaenia americana* Jewell, *Thubunaea leiopismaniae* Harwood, and *Oswaldocruzia leidy* Travassos.

The first station was located in Hermann Park within the city of Houston. The soil here consists entirely of Acadia clay, which is described by Geib, Bushnell and Bauer

¹ This investigation was made while the writer was in residence at Rice Institute, Houston, Texas.

('22) as follows: "The topsoil of Acadia clay is brownish-gray or light-gray stiff clay, showing some yellowish-brown mottling, usually reaching a depth of three feet. . . . Areas of this soil are flat or depressed, and drainage is poor. The substratum usually shows lime concretions in varying quantities. . . . Pine, willow oak, ash, and saw palmetto constitute the forest growth on this soil . . . with an undergrowth of youpon, blackberry briars, and carpet grass in the clearings." In Hermann Park the conditions answer very well to the above description. The area is very flat, and after heavy rains the water stands on much of it for several days. The acidity of the soil was tested by the colorimetric method and found to vary from a pH of 6.2 to 6.8. Table I shows the parasites found in the lizards from this station.

TABLE I. *Data on parasites found in hosts collected at various stations*

Date	No. examined	<i>Cylindro- taenia</i>	<i>Brachy- coelium</i>	<i>Thubunaea</i>	<i>Oswaldo- cruzia</i>
Station 1 (1929-30)					
23.II.	1	0	0	1	0
10.III.	4	0	3	1	0
20.IV.	7	2	0	2	0
23.V.	4	0	1	0	0
30.IX.	10	4	3	4	0
30.X.	10	4	1	2	0
27.XI.	10	6	2	3	0
29.XII.	2	2	0	0	0
20.II.	10	5	3	1	0
7.III.	10	4	3	2	0
31.III.	10	6	3	3	0
29.IV.	10	3	2	1	0
Total	88	36	21	20	0
Per cent	100	41	24	23	0
Station 2 (1930 and 1932)					
30.III.	11	0	4	3	5
30.VI.	11	0	5	0	7
Total	22	0	9	3	12
Per cent	100	0	41	14	54
Station 3 (1932)					
30.III.	4	0	2	0	0
1.IV.	12	0	3	0	0
4.V.	5	0	1	0	0
Total	21	0	6	0	0
Per cent	100	0	29	0	0
Station 4 (1932)					
8.IV.	11	3	1	4	0
8.VIII.	3	2	0	0	0
21.VIII.	1	0	0	0	0
Total	15	5	1	4	0
Per cent	100	33	7	27	0

Station 2 lies a few miles east of Houston where the Goose Creek road crosses Green's Bayou. The soil on this location is Acadia very fine sandy loam. It has been produced from Acadia clay by the so-called "ageing" process. In this process all lime concretions have disappeared except in the lower subsoil. The surface soil is a very fine sandy loam underlaid at a depth of about 18 inches by clay. According to Geib *et al.*

(1. c.), the forest growth consists principally of shortleaf pine, willow oak, sweet gum, post oak and water oak with blackberry briars, French mulberry and carpet grass in the clearings. On the plot of ground where the collecting was done there are also numerous examples of magnolia and cypress trees. This plot lies very close to the bayou and, as it is only a few feet above ordinary water level, it must be frequently inundated. There are also considerable areas occupied by low spots that are under water much of the year. The pH values are 5.8 to 6.4. Table I lists the parasites found.

Station 3 is a few miles west of Houston at a Boy Scout camp. The soil there is Acadia fine sandy loam. The surface is a little more sandy in texture than in Acadia very fine sandy loam and the lime concretions are even more scarce in the lower subsoils, but the chief differences lie in the physical features. Buffalo Bayou runs through the middle of this station, but this bayou has cut a deep ravine in the soil, and consequently the location where the collecting was done is so far above the ordinary stream level that it is seldom if ever flooded. The area is also cut by numerous tributary ravines, which form an excellent drainage system. Because of this well drained condition of the soil, magnolia and cypress are absent. The pH values of the Acadia fine sandy loam ranged from 5.8 to 6.4. Table I shows what parasites were found.

Station 4 lies west of Houston on the alluvial soils of the Brazos River Bottoms near Dewalt, Texas. The soil is a loamy clay of the Miller series, which Carter ('31) describes as follows: "The Miller soils have chocolate-red calcareous surface soils merging below with chocolate-red calcareous subsoils. The surface soils are a little darker in color and lighter in texture than the subsoils, but otherwise there is little difference. The soils are granular and work readily into a friable condition, while the subsoils, though fairly heavy, are permeable and of moderately open structure. . . . They occupy low flat valley positions in the flood plains and are overflowed occasionally." The trees on this soil consist mainly of elm, hackberry, ash, haw, pecan and some ash-leaved maple. The collecting was done in the wooded portion near the river banks. The pH values range from 7.8 to 8.2, the more acid soils coming from the low spots. Table I shows the parasites which were obtained at this station.

DISCUSSION

Before discussing these observations it may be well to mention that there was not any readily observable difference in the numbers of the lizards to be found at the various stations. It seems at once apparent that either the lighter soils are not favorable for the development of *Cylindrotaenia americana* or that the proper intermediate host does not occur on this type of soil. It must be remembered, however, that tapeworms with direct life histories are known. Joyeux ('24) gave evidence for believing that a South African tapeworm, which he refers to as *Cylindrotaenia americana* Jewell, possesses a direct life cycle. If this evidence is sound, it must be assumed that the lighter soils are unfavorable to the development of the species in question. However, it is very doubtful if Joyeux really had specimens of *C. americana*.

Brachycoelium daviesi is the most common of the parasites considered, but this parasite seems to be much less common in hosts at Station 4 than at the other stations. This is surprising when one considers the much greater abundance of snails in general at Station 4. However, certain varieties of snails are much commoner at the other three stations and it is easily possible that one of these varieties, rare at Station 4, is the intermediate host of *Brachycoelium daviesi*.

Thubunaea leiopismae seems to be less common in lizards on the sandy soils and the reason which first comes to mind is the lack of the proper intermediate host on these sandy soils.

Oswaldocruzia leidy was very common in hosts at Station 2 but nowhere else. It seems possible to explain this on the basis of two factors. As these worms were absent

in hosts obtained from the clay soils it may be assumed that the heavier soils do not furnish a favorable environment for the development of the free-living stages. On the other hand their absence from Station 3 was more probably due to the much drier conditions of the soils at this station.

Similar effects of soil types upon the distribution of the hookworm have been observed by various authors. Stiles ('03) first pointed out that hookworm disease in the southern United States was common in sandy soil areas, and rare or absent in clay soil areas. Later, Augustine and Smillie ('26) in Alabama, as well as Kerr and Richard ('26) in Tennessee, verified and extended these observations. Chandler found in Bengal that on very light porous soils with scanty rainfall there was less hookworm disease than on neighboring heavier soils. These observations have been well supported by numerous laboratory tests by several authors, so that there is well established evidence that in hookworm development the same factors are operative that here seem to have affected *Oswaldocruzia* adversely, namely, non-porous clay soils, and too dry porous soils. There is also reason to believe that *Oswaldocruzia*, like the hookworms and most bursate nematodes, has a free-living, preparasitic stage, but we cannot conclude that clay soils are similarly detrimental to all nematodes with free-living phases in their life cycles, since both *Cosmocercoides dukei* and *Kalicephalus agkistrodontis*, whose larvae hatch and undergo appreciable development in aqueous cultures, were very numerous on all four types of soil studied in this series.

Little further work has been done on the effect of soil on the distribution of parasites, but two more helminths may be mentioned in this connection. Chandler ('28) pointed out that human *Ascaris* and *Trichuris* infections become rare in very dry regions, the former being the more resistant to dryness. This has been corroborated in field and laboratory by several workers (Caldwell and Caldwell, '28; Spindler, '29; Nolf, '32). Even with *Cylindrotaenia*, *Brachycoelium* and *Thubunea* the moisture content of the soil may be the deciding factor, rather than lack of the proper intermediate hosts as suggested above.

SUMMARY

1. The helminth parasites of a lizard, *Leiolopisma laterale*, exhibited specific differences on four types of soil in the vicinity of Houston, Texas.
2. *Cylindrotaenia*, a cestode, is abundant in lizards living on clay soils, and absent in lizards living on sandy soils.
3. *Brachycoelium*, a trematode, though less common at one collecting station, was present in lizards living on all four types of soils considered in this paper.
4. *Thubunea*, a spiruroid nematode, was absent from lizards taken on a well drained sandy soil, but common in those hosts from a similar, though poorly drained soil, and abundant in host specimens taken on moist clay soils.
5. *Oswaldocruzia*, a bursate nematode, appeared only in lizards living on the poorly drained sandy soil.

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